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THE GENERA AND SUBGENERA OF DARTERS (PERCIDAE, ETHEOSTOMATINI)

By
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Since 1955 the generic and subgeneric classification of darters has been largely the concept of Reeve M. Bailey (Bailey, 1951; Bailey, Winn and Smith, 1954; Bailey and Gosline, 1955). As future studies and data will alter the classification presented herein, so are changes in Bailey's classification offered on the following pages. All proposed changes are subgeneric; the greater stability in nomenclature inherent in more inclusive genera argues for the continued use of Bailey's three-genus classification of darters rather than elevating some or all subgenera to generic status. More important contributions than the proposed changes are the morphological diagnoses of genera and subgenera incorporating characteristics examined critically, either in the literature or during this study, on each species of darter treated herein.

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METHODS

Phenetic and phylogenetic (cladistic) methods were employed in the following study on 142 species of darters (Appendix A) using 52 morphological characters (Appendix B). "The fundamental distinction between phenetic and phylogenetic methods is that the former group according to overall similarity while the latter unite taxa only on the basis of synapomorphy" (Mickevich, 1978).

Phenetic Method.—Phenetic similarities of 142 species of darters or some subset thereof were examined using CLUSTER, written by Dr. Richard B. Selander, University of Illinois. Phenograms were produced using three procedures: (1) data were standardized (mean = 0, standard deviation = 1), Pearson product-moment correlation coefficients were calculated as measures of similarity between OTU's (species), and OTU's were clustered using the UPGMA (unweighted pair-group method using arithmetic averages) (Sneath and Sokal, 1973); (2) data were transformed by ranging from 0 to 1, average taxonomic distances between OTU's were calculated, and OTU's were clustered using the UPGMA; (3) data were ranged, mean character differences between OTU's were calculated, and OTU's were clustered using UPGMA.

Cladistic Method.—Unrooted WAGNER networks (Kluge and Farris, 1969; Farris, 1970) were constructed using the "rootless" algorithm of Farris (1970). Cladograms were produced by rooting the networks (Farris, 1972) at the midpoint of the longest patristic distance separating any pair of OTU's or by the inclusion of *Perca flavescens* as an outgroup. The most parsimonious (shortest) cladograms are ones based on synapomorphies (Farris, Kluge and Eckardt, 1970).

Cophenetic correlation coefficients, which reflect the ability of a phenogram (or cladogram) to describe the distance matrix (Sneath and Sokal, 1973), are given in the figure legends.

Characters.—Characters selected for numerical analysis were those which varied among species but which were relatively constant within species. Characters exhibiting a large amount of intraspecific variation in at least some species (e.g. cheek and opercle squamation) and characters difficult to express numerically even when coded (e.g. body and fin colors) were not used. For morphometric data (meristic counts and body proportions) mean (or if so indicated in Appendix B, modal) values for each species were used as character states (Appendix C). For qualitative characters the various states were grouped into classes and assigned numerical values (coded).

Pectoral, pelvic and caudal fin lengths were lengths of the longest rays. Second dorsal and anal fin lengths were from the anterior point of origin of the fin to the posterior tip of the depressed fin. The distance from the origin of the second dorsal fin to the center of the base of the caudal fin (QL) was used as a basis for comparing second dorsal fin lengths. Interpelvic fin width was the distance between pelvic fin bases. Other counts and measurements were made following Hubbs and Lagler (1958) or as modified by Page (1974). Lateralis terminology follows Page (1977). When sexual dimorphism was evident in a character, specimens of only one sex were used or the feature was divided into two characters. The biochemical characters used in the numerical analysis of *Percina* (Page, 1974) were not used in this study because data were missing for about one-half of the species. Vertebral counts also were not used because data are unavailable for many species. The 52 characters employed were distributed as follows:

I. Quantitative		33
A. Meristic	17	
B. Body proportions	16	
II. Qualitative		19
A. Pigmentation	2	
B. Squamation	6	
C. Miscellaneous	11	

Of the 52 characters, 42 were continuously variable, multistate characters. The other 10 were two-state characters utilizing a derived character state found in one or more species.

Systematics.—Phenograms and cladograms were compared to the existing generic and subgeneric classification [that of Bailey and Gosline (1955) modified subsequently by Collette and Yerger (1962), Cole (1967), Page and Whitt (1973a), Page (1974), and Williams and Robison (1980) (Table 1)] and discordances considered as potential errors in classification. Examination of synapomorphous (shared derived) characteristics as evidence of relationship (sensu Hennig, 1966) sometimes involved characters not included in the numerical analysis because of extreme difficulty in coding (e.g., colors in first dorsal fin).

TABLE 1.—Classifications of darters.

Genera and Subgenera of Bailey and Gosline (1955)	Modifications Subsequent to Bailey and Gosline (1955)	Classification Adopted Herein (and Number of Described Species in Each Subgenus)
Percina		*Percina*
Hadropterus		*Hadropterus* (4)
Swainia		*Swainia* (4)
Alvordius		*Alvordius* (8)
Ericosma		*Ericosma* (2)
	Odontopholis (Page, 1974)	*Odontopholis* (1)
Hypohomus		*Hypohomus* (1)
Cottogaster		*Cottogaster* (1)
Imostoma		*Imostoma* (5)
Percina		*Percina* (5)
Ammocrypta		*Ammocrypta*
Crystallaria		*Crystallaria* (1)
Ammocrypta		*Ammocrypta* (6)
Etheostoma		*Etheostoma*
Psychromaster		*Psychromaster* (1)
	Litocara (Page and Whitt, 1973a)	*Litocara* (2)
Allohistium		*Allohistium* (1)
Etheostoma		*Etheostoma* (13)
Ulocentra		*Nanostoma* (6)
	Doration (Cole, 1967)	*Doration* (2)
Boleosoma		*Boleosoma* (5)
Ioa		*Ioa* (1)
	Vaillantia (Cole, 1967)	*Vaillantia* (2)
Nothonotus		*Nothonotus* (13)
		Fuscatelum (1)
		Belophlox (3)
	Villora (Collette and Yerger, 1962)	*Villora* (1)
	Ozarka (Williams and Robison, 1980)	*Ozarka* (5)
Austroperca		
Oligocephalus		*Oligocephalus* (15)
Catonotus		*Catonotus* (10)
Hololepis		*Boleichthys* (10)
Microperca		

RESULTS

Comparisons of Methods.—Comparisons among phenograms and cladograms of a given group of species were made by comparing their structures to the existing classification of darters, by examining their overall ability to form clusters, and by contrasting their cophenetic correlation coefficients (CPCC) (Table 2).

The objective in doing a numerical taxonomic study is to examine and improved the existing classification of a group of organisms. The lack of congruence among phenograms and cladograms prevents the substitution of any one of them as the structure for a new classification and instead requires that they be compared with the existing classification, which generally is a product of careful study.

TABLE 2.—Comparisons of numerical taxonomic methods.

	Cophenetic correlation coefficient	No. subgenera clustered[1]	Clustering above subgenus
I. *Percina* (34 species)			
1. UPGMA—average taxonomic distance	0.810	5	good
2. UPGMA—mean character difference	0.784	4	good
3. UPGMA—correlation coefficient	0.898	6	good
4. WAGNER—rooted at midpoint	0.880	6	good
5. WAGNER—rooted with outgroup	0.840	3	good
II. *Etheostoma* (101 species)			
1. UPGMA—average taxonomic distance	0.800	3	poor
2. UPGMA—mean character difference	0.772	4	poor
3. UPGMA—correlation coefficient	0.803	4	good
4. WAGNER—rooted at midpoint	0.817	4	fair
5. WAGNER—rooted with outgroup	0.784	2	fair
III. *Percina, Ammocrypta* and *Etheostoma* (142 species)			
1. UPGMA—average taxonomic distance	0.820	5	poor
2. UPGMA—mean character difference	0.781	8	poor
3. UPGMA—correlation coefficient	0.798	12	good
4. WAGNER—rooted at midpoint	0.786	6	fair
5. WAGNER—rooted with outgroup	0.836	6	fair

[1] Excluding monotypic subgenera.

The "errors" in classification which are suggested most consistently by the phenograms and cladograms are ones to receive the most attention. Conversely, the numerical taxonomic method which gives a structure most similar to the existing classification is likely to be the best in terms of information content, and is the one which a specialist on the taxonomic group under study will consider the most reliable. Among procedures used, UPGMA—correlation coefficient gave results most congruent with darter systematics and WAGNER—rooted with an outgroup gave the least congruent results (Table 2). For small groups of species (Figs. 1-4) WAGNER—rooted at midpoint generally gave results as good as those of UPGMA—correlation coefficient, but it gave poor results when all species were included (Table 2). Sneath and Sokal (1973), comparing only phenetic methods, noted that when comparisons are made with existing classifications, structures produced from procedures using correlation coefficients usually are deemed the best.

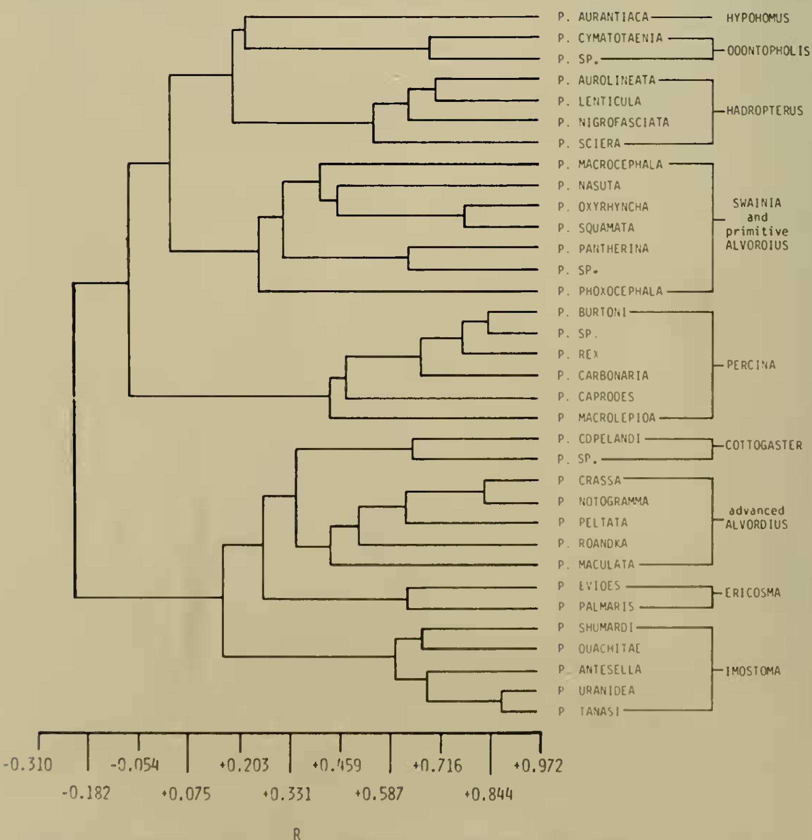

Fig. 1.—Phenogram of 34 species of *Percina*. UPGMA—correlation coefficient; CPCC = 0.898.

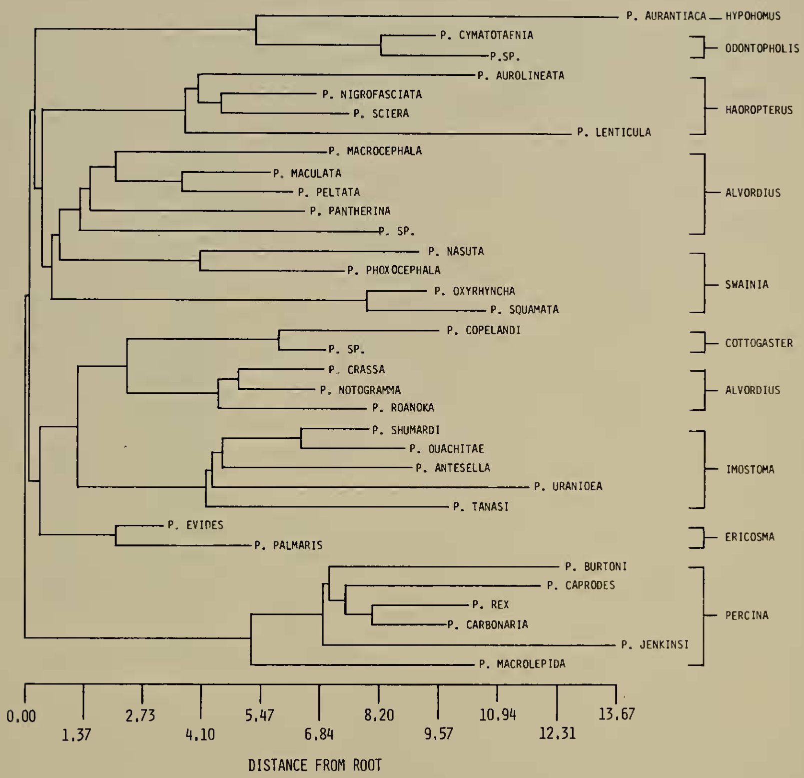

Fig. 2.—Cladogram of 34 species of *Percina*. WAGNER—rooted at midpoint; CPCC = 0.880.

For *Percina,* with only 34 species and distinct subgenera (Page 1974), all procedures clustered well. For larger groups of species, UPGMA—correlation coefficient consistently formed large clusters from small clusters (Figs. 1, 3, 5, 7). These structures resemble conventional taxonomic classifications and, in fact, resemble fairly closely the existing classification of darters. Phenograms based on average taxonomic distance and mean character difference successively added OTU's to existing clusters (Fig. 6). Their structures do not suggest relationships beyond those involving only a few species and do not yield themselves as well as UPGMA—correlation coefficient phenograms to a meaningful comparison to existing taxonomy. WAGNER procedures (Figs. 2 and 4) clustered better than did UPGMA—average taxonomic distance and UPGMA—mean character difference but not as well as UPGMA—correlation coefficient.

Generally, UPGMA—correlation coefficient and WAGNER—rooted at midpoint produced the highest CPCC's and UPGMA—

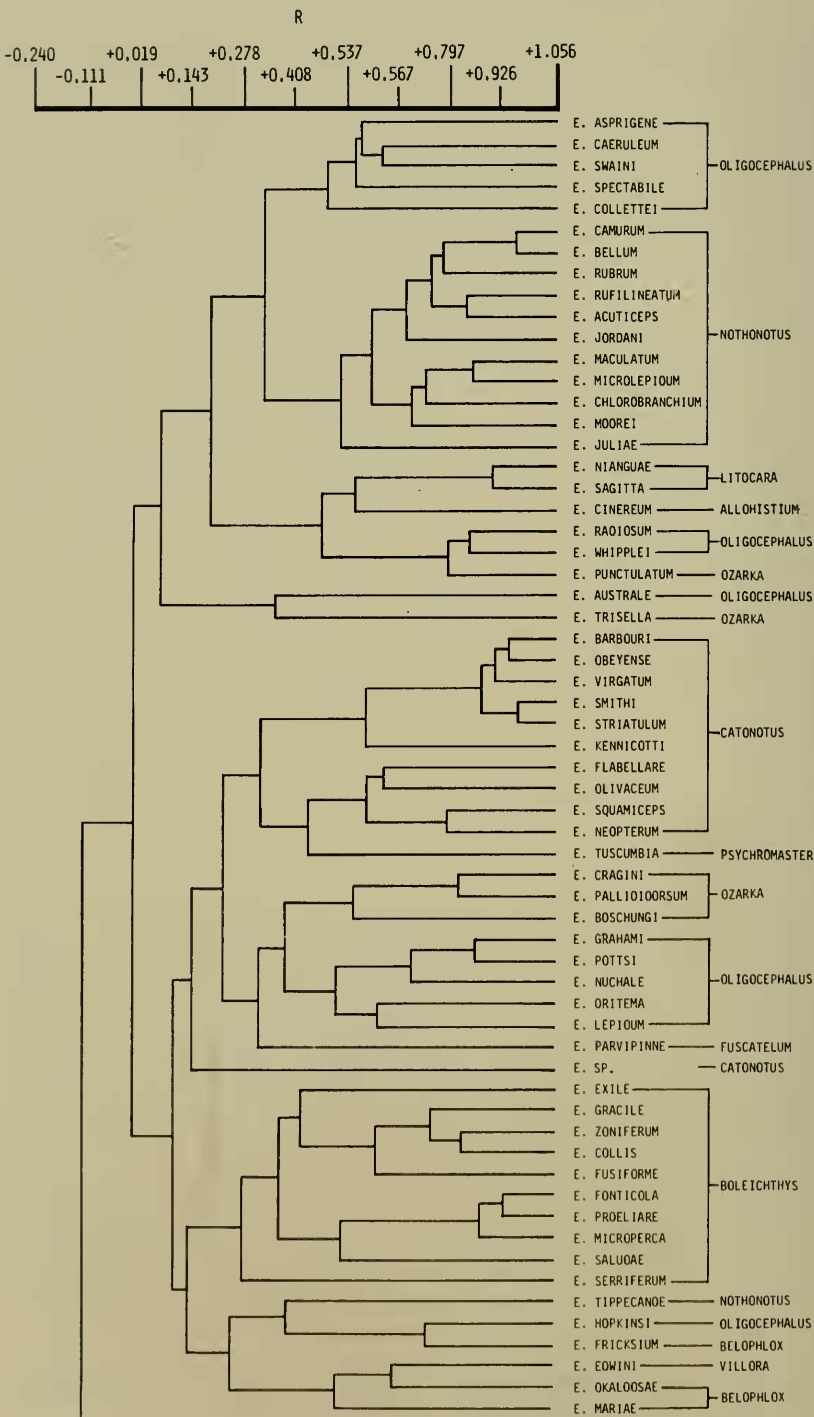

Fig. 3a.—Upper part of phenogram of 101 species of *Etheostoma.* UPGMA —correlation coefficient; CPCC = 0.803. Subgeneric assignments are based on conclusions herein.

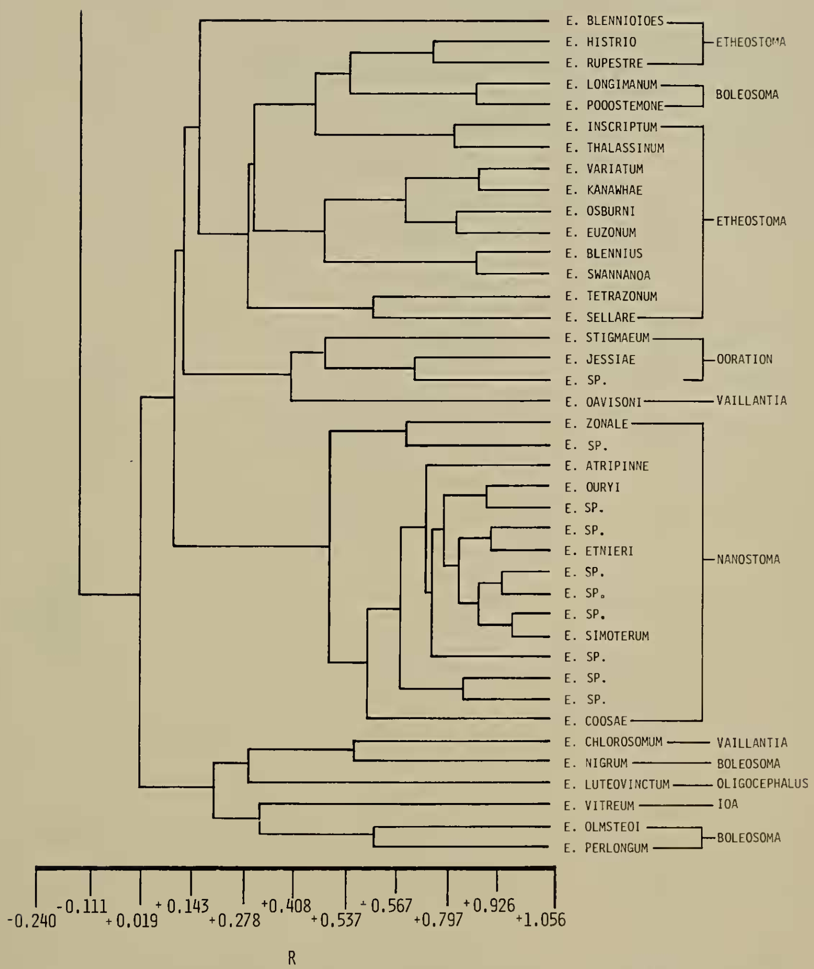

Fig. 3b.—Lower part of phenogram of 101 species of *Etheostoma*. UPGMA —correlation coefficient; CPCC = 0.803. Subgeneric assignments are based on conclusions herein.

mean character difference produced the lowest. However, CPCC did not consistently rate one procedure over another.

Systematics.—A phenogram of all 142 species of darters examined (Fig. 5) showed many similarities to the classification of Bailey and Gosline (1955); at a clustering coefficient of approximately 0.60, many of their subgenera were delimited.

The final cluster among the 142 species, rather than a union of genera, was a union of the "primitive darters" (including all species of *Percina* and *Ammocrypta* and many species of *Etheostoma*) and the "advanced darters" (including only species of *Etheostoma*).

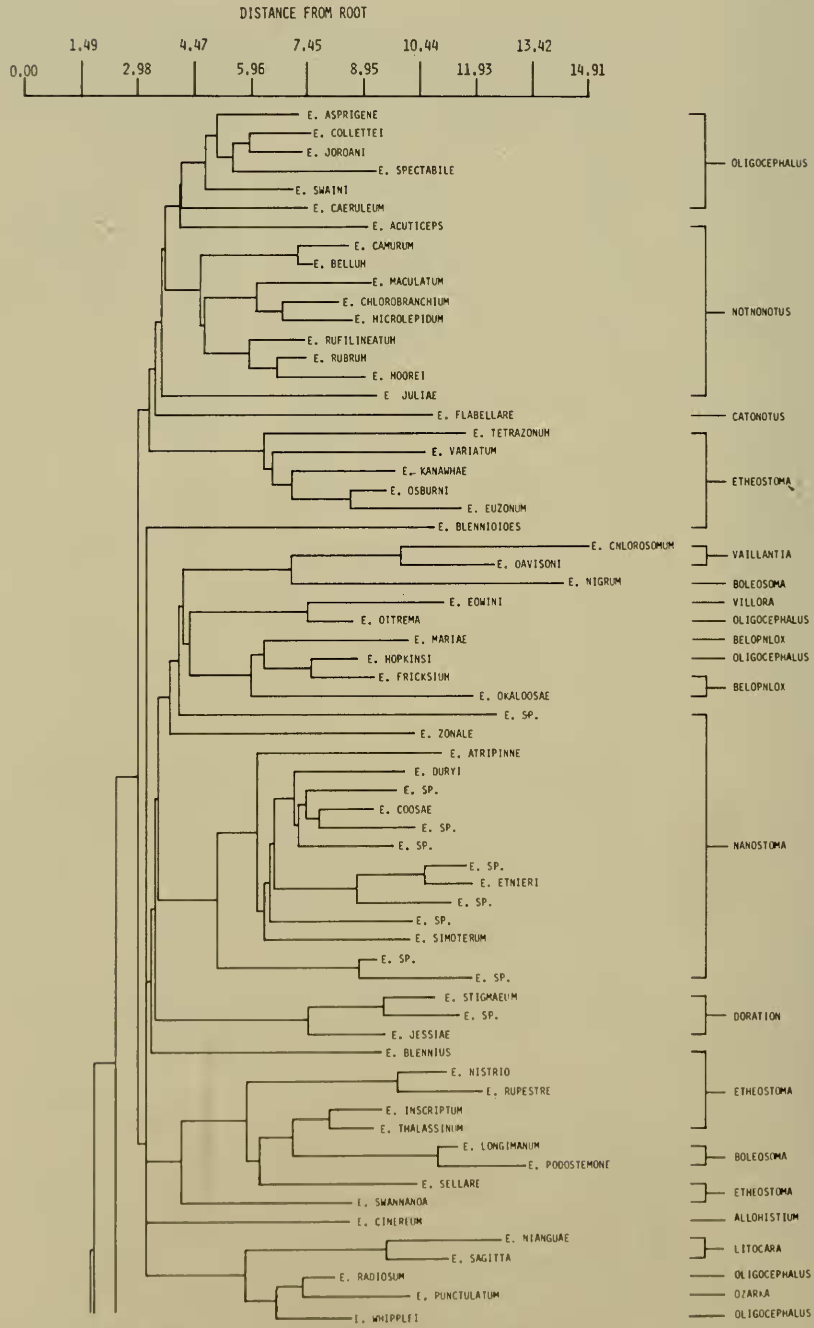

Fig. 4a.—Upper part of cladogram of 101 species of *Etheostoma*. WAGNER—rooted at midpoint; CPCC = 0.817. Subgeneric assignments are based on conclusions herein.

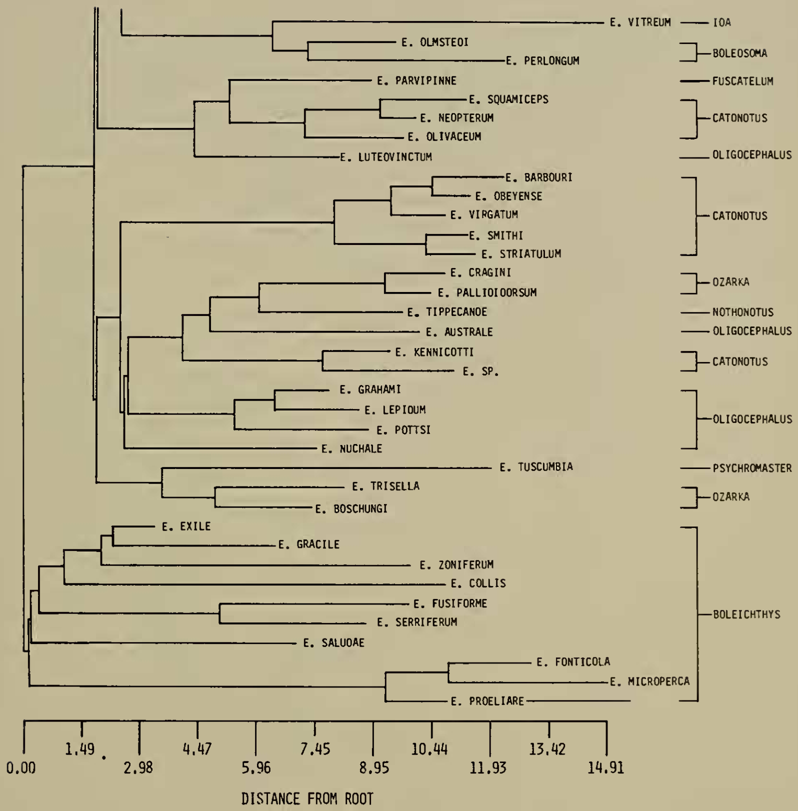

Fig. 4b.—Lower part of cladogram of 101 species of *Etheostoma.* WAGNER—rooted at midpoint; CPCC = 0.817. Subgeneric assignments are based on conclusions herein.

Contained in the primitive group of darters were species of *Etheostoma* usually assigned to the subgenera *Allohistium, Ioa, Litocara, Etheostoma, Ulocentra,* and *Doration.* Included in the advanced group were species of *Oligocephalus, Nothonotus, Catonotus, Psychromaster, Austroperca, Villora, Hololepis,* and *Microperca. Boleosoma* and *Vaillantia* were split among the two major groups.

Subgenera of *Percina* grouped in agreement with the classification presented by Page (1974) except that *Swainia* and *Alvordius* failed to group as distinct entities (Fig. 5). This is surprising in that *Swainia* is distinct and easy to diagnose from other subgenera of *Percina. Alvordius* consists of nine species,[1] including among the most primitive *(P. macrocephala)* and advanced *(P. roanoka)* spe-

[1] *Percina gymnocephala* Beckham 1980 was described after computer analyses were completed.

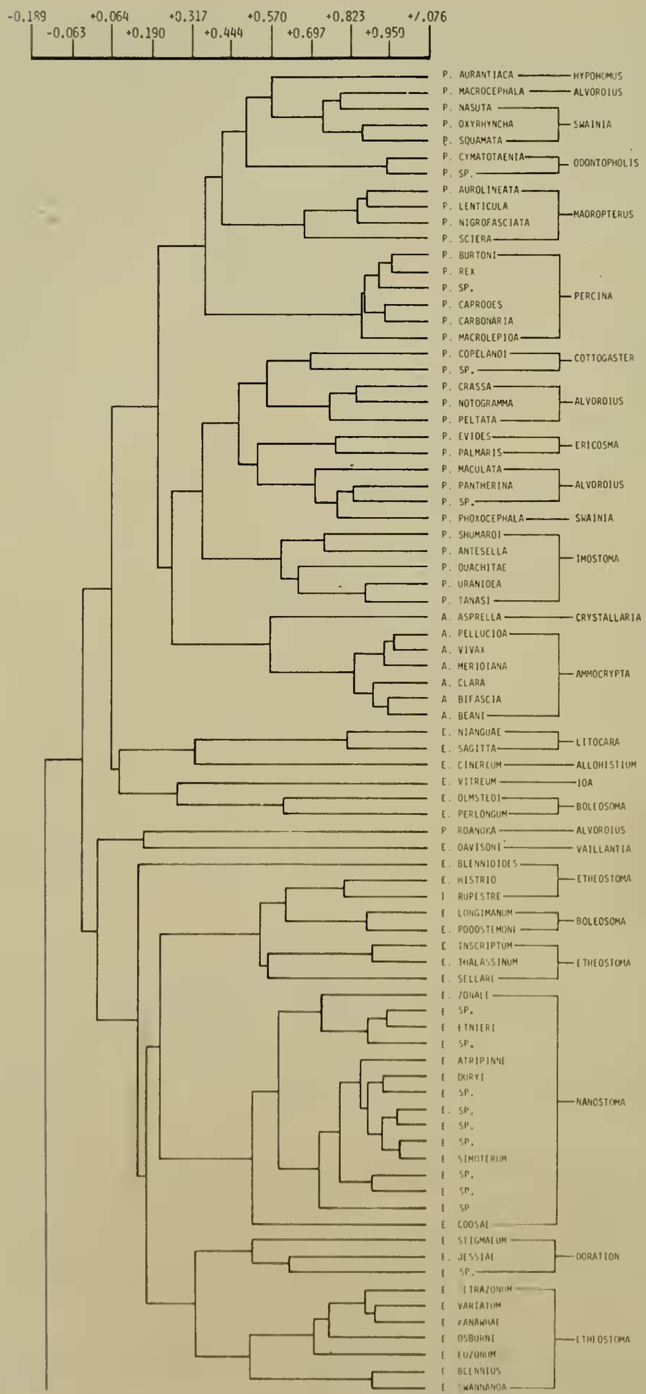

Fig. 5a.—Upper part of phenogram of 142 species of darters. UPGMA—correlation coefficient; CPCC = 0.798. Subgeneric assignments are based on conclusions herein.

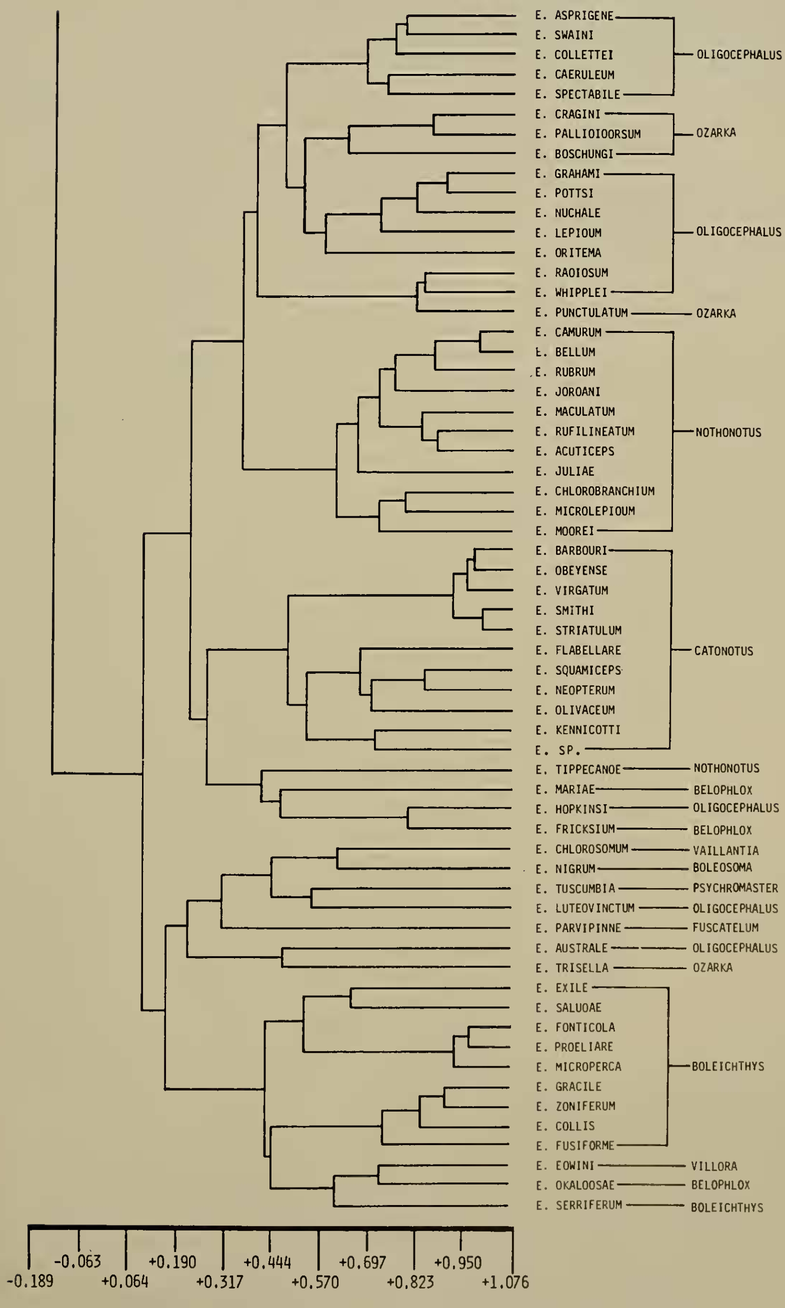

Fig. 5b.—Lower part of phenogram of 142 species of darters. UPGMA—correlation coefficient; CPCC = 0.798. Subgeneric assignments are based on conclusions herein.

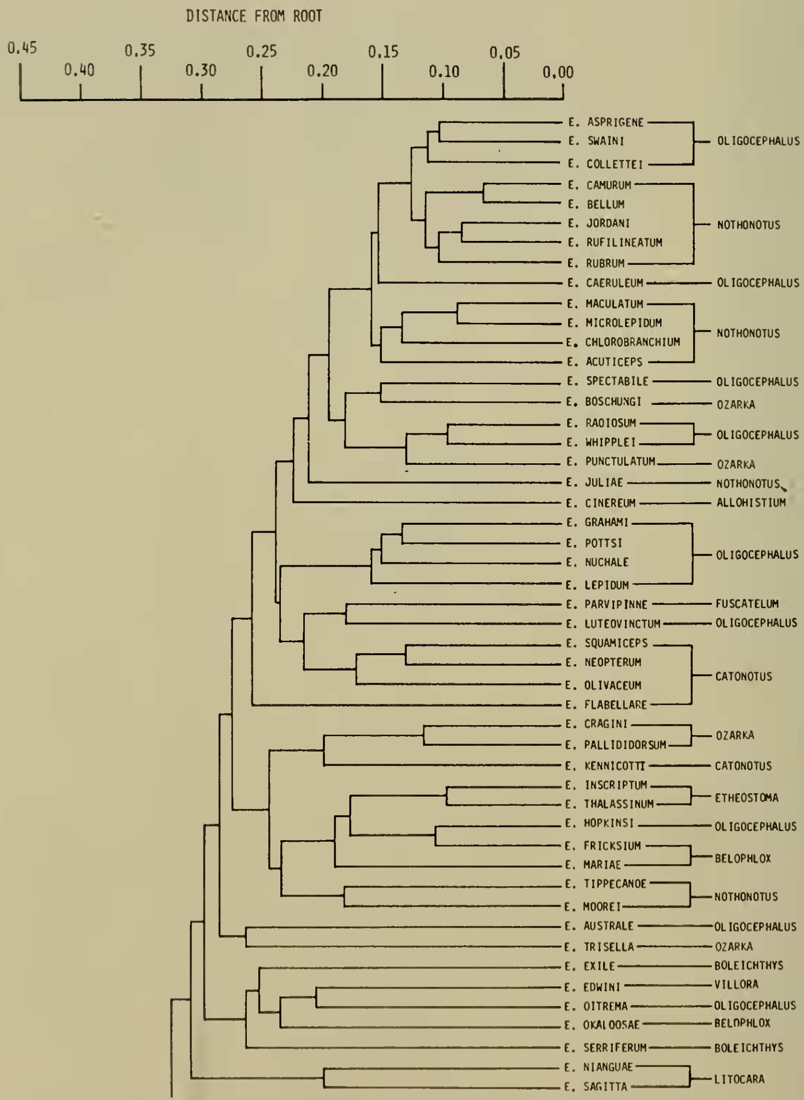

Fig. 6a.—Upper part of phenogram of 101 species of *Etheostoma*. UPGMA —average taxonomic distance; CPCC = 0.800. Subgeneric assignments are based on conclusions herein.

cies of *Percina*, and this large array of evolutionary gradation is presumably responsible for the failure of the species to cluster. *P. roanoka* is a highly evolved form that joined the *Percina* cluster after species of *Ammocrypta* and *Etheostoma* (Fig. 5). This species is adapted for life in shallow rocky riffles, a unique attribute among *Percina*, and consequently has unusual morphological character-

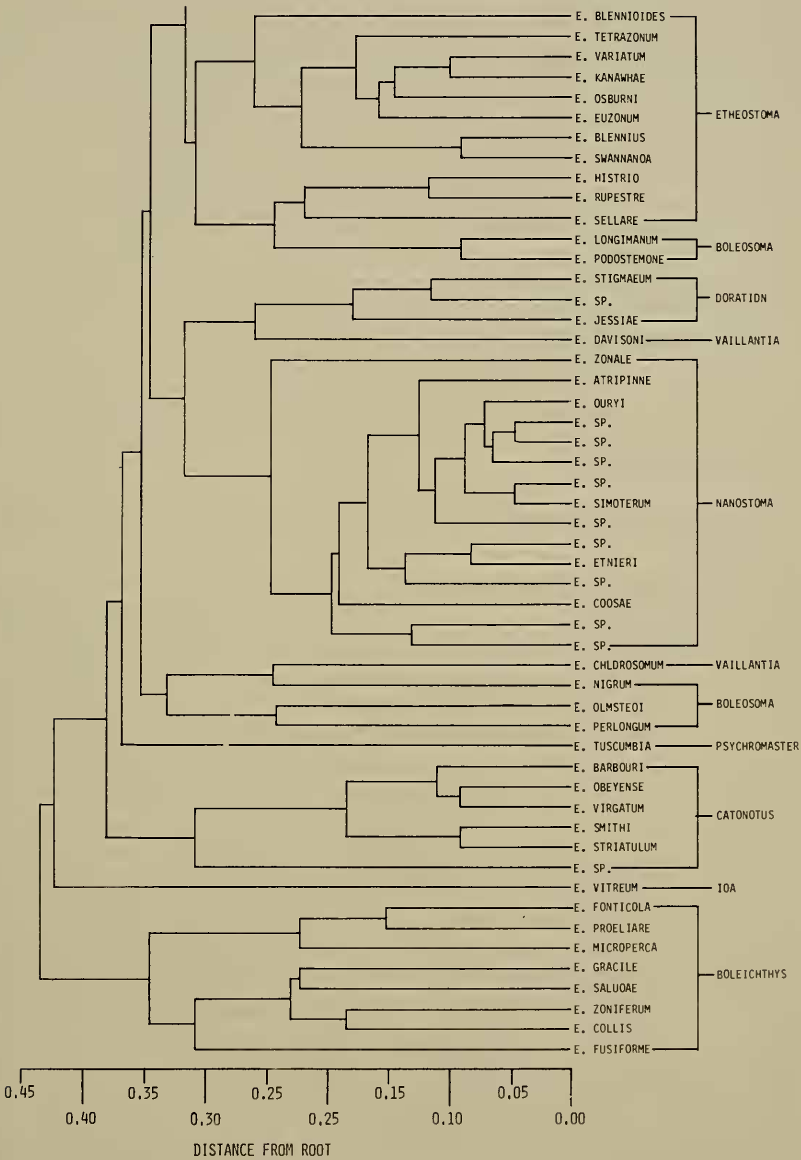

Fig. 6b.—Lower part of phenogram of 101 species of *Etheostoma*. UPGMA —average taxonomic distance; CPCC = 0.800. Subgeneric assignments are based on conclusions herein.

istics. However, *P. roanoka* clearly is related to other Atlantic drainage species of *Alvordius* (Mayden and Page, 1979).

A phenogram and a cladogram of species of *Percina* only (Figs. 1 & 2) also failed to segregate *Swainia* and *Alvordius* as discrete

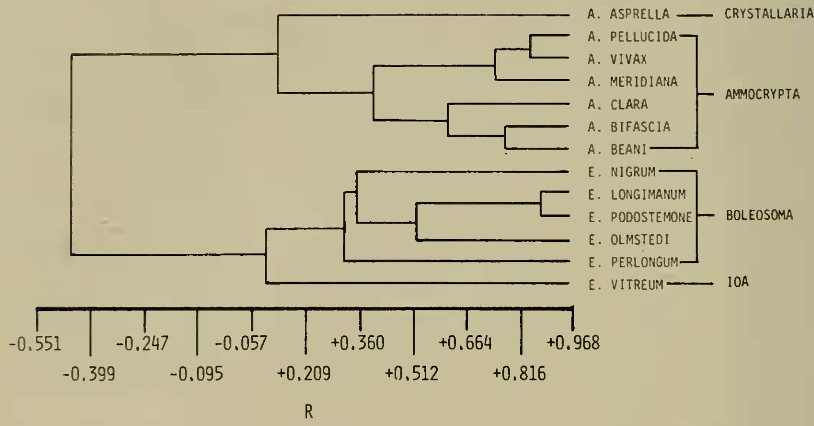

Fig. 7.—Phenogram of 13 species of the subgenera *Crystallaria, Ammocrypta, Ioa* and *Boleosoma.*

units but included *P. roanoka* in clusters containing other species of *Alvordius.*

Questions about the wisdom of lumping darters into only three genera specifically have concerned the relationship of the logperches (*Percina* s.s.) to other species of *Percina* s.l. (e.g., Stevenson, 1971), the relationship of *asprella* to other *Ammocrypta* (Moore, 1968; Miller and Robison 1973), and the relationship of *vitreum* to other species of *Etheostoma* and to species of *Ammocrypta* (Page and Whitt, 1973a). The inclusion of logperches in a genus with other darters having modified scales on the venter is discussed by Page and Whitt (1973b) and is further supported by the phenograms generated during the present study (Figs. 1 & 5).

The inclusions of *asprella* in the genus *Ammocrypta* and *vitreum* in *Etheostoma* are supported by the phenogram of all species (Fig. 5) and by a phenogram (Fig. 7) including only the subgenera *Ammocrypta, Crystallaria, Boleosoma,* and *Ioa.* As shown, the affinity of *vitreum* is to species of *Etheostoma* rather than to *Ammocrypta,* and *asprella* is as close phenetically to species of the subgenus *Ammocrypta* as *vitreum* is to the subgenus *Boleosoma* of *Etheostoma. Boleosoma* was selected as the test-group of *Etheostoma* because of the assumed relationship between *E. vitreum* and species of *Boleosoma* (Winn and Picciolo, 1960; Collette, 1965; Jenkins, 1971).

Species of *Ammocrypta* clustered in two distinct groups (Figs. 5 & 7), supporting the disubgeneric classification of Bailey and Gosline (1955).

The affinities among species of *Etheostoma* shown by the phenogram of all species (Fig. 5) were in general agreement with the existing classification (Table 1). Discordances were the following.

1. Species of the subgenus *Etheostoma* failed to cluster and instead were divided into four groups:

   a. *E. zonale* clustered with species of *Ulocentra* (labeled as *Nanostoma* in Fig. 5),
   b. *E. blennioides,*
   c. *E. variatum, E. tetrazonum, E. kanawhae, E. osburni, E. euzonum, E. blennius, E. swannanoa,*
   d. *E. histrio, E. rupestre, E. inscriptum, E. thalassinum, E. sellare.*

2. Species of the subgenus *Boleosoma* failed to cluster and were widely dispersed over the phenogram in three groups:

   a. *E. longimanum* and *E. podostemone* clustered with species of the subgenus *Etheostoma.*
   b. *E. nigrum* clustered with *E. chlorosomum,*
   c. *E. perlongum, E. olmstedi.*

3. The two species of *Vaillantia (chlorosomum, davisoni)* failed to cluster.

4. The two species of *Psychromaster (tuscumbia, trisella)* failed to cluster.

5. *E. tippecanoe* failed to cluster with other species of *Nothonotus.*

6. Species of the subgenus *Oligocephalus* failed to cluster and instead were divided into six groups:

   a. *E. lepidum* group with 16 species (Fig. 5),
   b. *E. juliae* clustered with species of *Nothonotus,*
   c. *E. mariae, E. fricksium, E. hopkinsi,*
   d. *E. luteovinctum,*
   e. *E. parvipinne,*
   f. *E. exile* clustered with species of *Hololepis (fusiforme, serriferum, gracile, zoniferum, collis, saludae), Microperca (microperca, proeliare, fonticola),* and *Villora (edwini, okaloosae).*

7. Species of *Villora* were within a large cluster formed mainly of species of *Hololepis.*

8. Species of *Microperca* were within a large cluster formed mainly of species of *Hololepis.*

A phenogram (Fig. 3) involving only species of *Etheostoma* again produced most of the discordances cited above except that species of *Etheostoma* (s.s.) with the exception of *E. zonale* (which still clustered with species of *(Ulocentra)* clustered; the *E. lepidum* group of *Oligocephalus* (16 species in Fig. 5) split into three groups, one of which was joined by the previously disjunct *E. parvipinne*; and species of *Villora* were clustered with the *E. mariae* group rather than with species of *Hololepis* and *Microperca.* The only additional disagreement with existing classification was the inclusion of *E. tuscumbia* in the cluster of species of *Catonotus.*

Considering discordances consistent in both phenograms (Figs. 3 & 5), the following questions concerning subgeneric relations are discussed.

1. Are the closest affinities of *E. zonale* with species of *Etheostoma* (s.s.) or *Ulocentra*?

The subgenera *Etheostoma* and *Ulocentra* are closely related and difficult to diagnose from one another. Bouchard (1977) tabulated eight distinguishing characteristics but indicated large overlap between the two subgenera. The most useful of those eight and additional characteristics for separating the two subgenera are given in Table 3. There is overlap in several of these characteristics but little to no overlap in the means of three body proportions (Fig. 8). In all three proportions *E. zonale* clearly belongs with species referred to *Ulocentra* (i.e., *E. zonale* has a very short snout in relation to body depth, a narrow head in relation to standard length, and narrow interpelvic width in relation to the length of the pelvic fin base). Furthermore, the least rejected phylogeny (sensu Wiley, 1975) based on characteristics in Table 3 demonstrates (Fig. 9), as did the phenograms (and cladograms, although more loosely—e.g. Fig. 4), that if two subgenera are to be recognized, *E. zonale* must be allied taxonomically to species of *Ulocentra* and not of *Etheostoma*. The inclusion of *E. zonale* means that *Nanostoma*, as the oldest available genus-group name, replaces *Ulocentra*.

TABLE 3.—Characteristics distinguishing the subgenera *Etheostoma* and *Ulocentra*, and comparisons with *E. zonale*.

	Etheostoma[1]	*Ulocentra*[2]	*E. zonale*
Breeding tubercles	present (except in *histrio, rupestre, sellare*)	absent	absent
Modal no. branchiostegal rays	6	5 (6 in *coosae*)	5
Modal no. preoperculomandibular pores	10 (9 in *histrio, rupestre*)	9 (10 in *coosae*)	10 (9 in some populations
No. dorsal saddles	usually 4 to 7	usually 8 or 9	usually 6
Snout length/body depth	0.36-0.50	0.27-0.33	0.30
Head width/standard length	0.140-0.165	0.125-0.140	0.135
Interpelvic fin width/ pelvic fin base length	0.61-0.85	0.28-0.61	0.45
Prevomerine teeth	present (except in *blennioides* and some *rupestre*)	absent (except in *coosae*)	present

[1] Included species are *E. blennioides, E. blennius, E. euzonum, E. histrio, E. inscriptum, E. kanawhae, E. osburni, E. rupestre, E. sellare, E. swannanoa, E. tetrazonum, E. thalassinum*, and *E. variatum*.

[2] *E. atripinne, E. coosae, E. etnieri, E. duryi, E. simoterum*, and nine undescribed species (Appendix A).

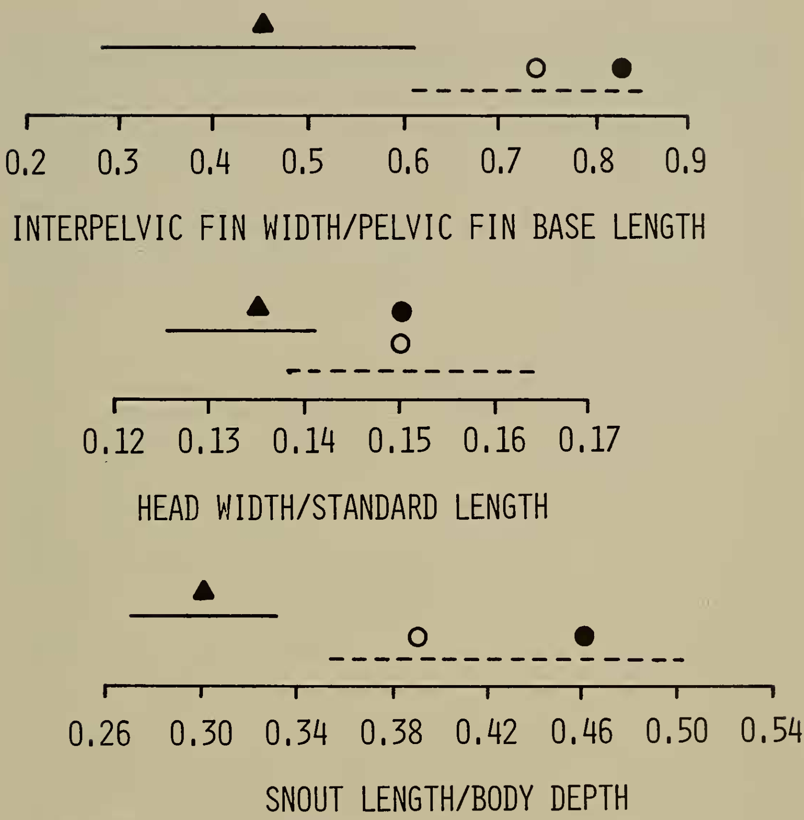

Fig. 8.—Means of fin and body proportions among species of *Ulocentra* (sensu Bailey and Gosline, 1955) and *Etheostoma* (s.s.). Solid line is range in means of *Ulocentra*; dashed line, range in means of *Etheostoma*. Triangle represents mean for *E. zonale*; dot, mean for *E. rupestre*; open circle, mean for *E. histrio*. The latter two species have been assumed to be close relatives of *E. zonale* (Tsai and Raney, 1974).

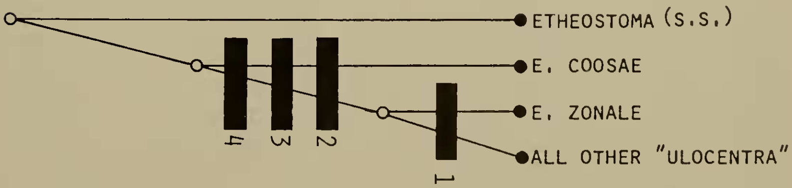

Fig. 9—Least rejected phylogenetic hypothesis of the relationships among species usually referred to the subgenera *Etheostoma* and *Ulocentra*. Synapomorphous characteristics (black rectangles) from Table 3 are (1) presence of 5 branchiostegal rays, (2) snout length/body depth = 0.27-0.33, (3) head width/standard length = 0.125-0.140, and (4) interpelvic width/pelvic fin base length = 0.28-0.61.

E. zonale probably originated near the time of the phylogenetic separation of *Etheostoma* (s.s.) and *Nanostoma* and consequently is somewhat intermediate between the two groups. The presence of five branchiostegal rays in all species of *Nanostoma* except *E. coosae* is the principal basis for taxonomic separation from *Etheostoma*. However, the sixth branchiostegal ray in many species of *Etheostoma* (s.s.) is often rudimentary, further suggesting the close relationship between the two groups of species. The alternative to recognizing *E. zonale* and all species of "*Ulocentra*" as members of *Nanostoma* would be to incorporate all species involved into the subgenus *Etheostoma*.

2. Are the closest affinities of *E. longimanum* and *E. podostemone* with species of *Boleosoma* or *Etheostoma* (s.s.), and

3. Are *E. nigrum* and *E. chlorosomum* closest relatives?

In the phenograms and cladograms (Figs. 3-6), *E. podostemone* and *E. longimanum* clustered with species of *Etheostoma* (s.s.), and *E. nigrum* clustered with *E. chlorosomum*. Fortunately all five species of *Boleosoma (podostemone, longimanum, nigrum, olmstedi, perlongum)* share a complex, derived characteristic that is solid evidence of common ancestry. That characteristic is the flattened bifurcate genital papilla of the female (Cole, 1967). Females of *E. chlorosomum* and species of *Etheostoma* (s.s.) do not have similar papillae.

Species of *Boleosoma* display a great deal of interspecific variation in physiognomy (as extremes, *E. perlongum* is long and slender and *E. longimanum* and *E. podostemone* are robust) and meristic counts, and this variation is probably responsible for the failure of the species to cluster. Character states in three body and fin proportions illustrate the extreme variation within *Boleosoma*: among all 142 species of darters examined, the mean HW/SL varied from 0.10 to 0.16, and among the five species of *Boleosoma* varied from 0.12 to 0.16 (70 percent of the range in states among all darters); similarly the range in mean CPD/SL among *Boleosoma* was 67 percent of that among all darters, and in D2FL/QL ♂ was 69 percent.

4. Should *E. chlorosomum* and *E. davisoni* be in separate subgenera? *E. chlorosomum* and *E. davisoni*, according to Howell (1968) members of the ditypic subgenus *Vaillantia*, failed to cluster in the phenograms. *E. davisoni* is superficially similar to *E. stigmaeum* and clustered with the subgenus *Doration* in one phenogram (Fig. 3). *E. davisoni* twice has been in the synonymy of *E. stigmaeum* (Jordan and Evermann, 1896; Bailey, Winn and Smith, 1954). *E. chlorosomum* clustered with *E. nigrum*, as discussed above.

In a phenogram comparing only *Vaillantia*, *Doration*, *Boleosoma*, and *Ioa* (the first three were lumped into one subgenus by Bailey and Gosline, 1955), *E. chlorosomum* and *E. davisoni* clustered as a unit. The two species are similar in physiognomy and share two synapomorphous characteristics: a bulb-shaped female genital papilla with villi around the pore (Howell, 1968) and fusion of the preorbital bars into a continuous black bridle around the snout. Both *E. chlorosomum* and *E. davisoni* modally have 10 dorsal rays (the only other species of *Etheostoma* having 10 or fewer are three species of *Boleichthys,* sec below), a mean BD/SL ratio of 0.15 (only three other species of *Etheostoma* have a ratio this small or smaller), a D2FL/QL ♂ ratio of less than 0.58 (true of only three other species of *Etheostoma*), and a D2FL/QL ♀ ratio of less than 0.54 (true of only two other species of *Etheostoma*). The failure of the two species to cluster in the larger phenograms (Figs. 3 & 5) is an enigma, but they share the above derived characteristics and both should be retained in the subgenus *Vaillantia.*

5. Should *E. tuscumbia* and *E. trisella* be in separate subgenera?

The addition of *E. trisella* to the previously monotypic *Psychromaster* (Bailey and Richards, 1963) was based on the only available specimen of *E. trisella,* the juvenile holotype. Considering the data now available on many more specimens of *E. trisella,* no reason exists to conclude that the species is closely related to *E. tuscumbia.* Both species modally have only one anal spine, but so do several other species of *Etheostoma.* In the phenograms, *E. trisella* is loosely allied to *E. australe* but probably is not intimately related. It appears in general appearance (physiognomy and stippled color pattern) to be most similar to the *E. punctulatum* species group *(E. punctulatum, E. cragini, E. pallididorsum, E. boschungi);* these five species were recently placed in the subgenus *Ozarka* (Williams and Robison, 1980). Recently acquired and as-yet unpublished data on reproduction in *E. trisella* reveal that it has the same highly specialized site of egg deposition (M. G. Ryon, pers. comm.) as that of *E. boschungi* (seepage water in pastures—Boschung, 1979).

In the phenogram of species of *Etheostoma* (Fig. 3), *E. tuscumbia* clustered with *Catonotus.* There are general similarities in physiognomy between *E. tuscumbia* and members of the *E. squamiceps* species group of *Catonotus* but no indicators of close relationship. The scales on the branchiostegal membranes and on top of the head, the long and tubular genital papilla of the male, tubular genital papilla of the female, and one anal spine separate *E. tuscumbia* from species of *Catonotus.* It seems prudent to maintain the highly singular *E. tuscumbia* in a monotypic subgenus.

6. Should *E. tippecanoe* be removed from *Nothonotus*?

Zorach (1972) considered *E. tippecanoe* an early offshoot of the *Nothonotus* lineage and tabulated several characteristics separating that species from other members of the subgenus. Early divergence and subsequent specializations apparently are responsible for the failure of *E. tippecanoe* to cluster with other *Nothonotus*. Although divergent, no compelling reason exists to separate *E. tippecanoe* from *Nothonotus* and in doing so to obscure the relationships of the species.

7. Are the closest affinities of *E. juliae* with species of *Oligocephalus* or *Nothonotus*?

Atypically for *Nothonotus*, *E. juliae* has broadly connected branchiostegal membranes and a fully scaled nape. It also lacks the blue-green breast and red spots on the side of the body typical of most (but not all) species of *Nothonotus*. However, *E. juliae* has the distinctive thin, alternating dark and light lines along the side of the body found in all *Nothonotus* except *E. tippecanoe* and *E. jordani* and absent in all *Oligocephalus*, and has a complete (over 95 percent pored) lateral line as do all *Nothonotus* except *E. tippecanoe*; all *Oligocephalus* except *E. mariae* and *E. fricksium* have incomplete lateral lines. *Nothonotus* are generally deeper bodied than are *Oligocephalus*, and *E. juliae* and *E. acuticeps* are extreme in this characteristic (Fig. 10). *Nothonotus* characteristically have a smaller D2L/D1L ratio than do *Oligocephalus* and *E. juliae* is typical for *Nothonotus* in this respect (Fig. 10).

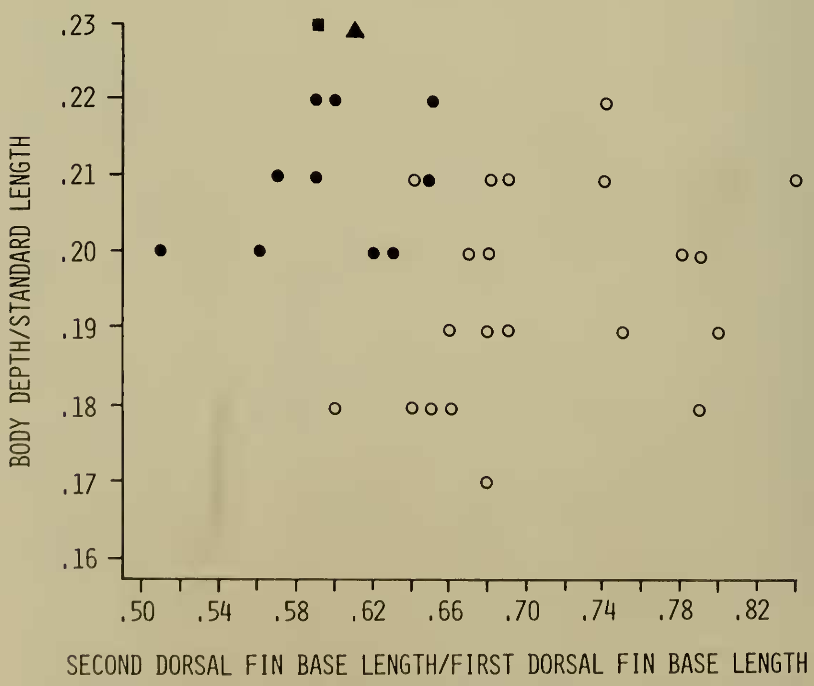

Fig. 10.—Scattergram of species of *Oligocephalus* sensu Bailey and Gosline (1955) (circles) and *Nothonotus* (dots, *E. acuticeps* = square, *E. juliae* = triangle) based on means of two proportional characteristics.

Oligocephalus and *Nothonotus* are difficult to separate diagnostically (Bailey, 1959; Zorach, 1972) because of the variation within each subgenus, but it is apparent that *E. juliae* is related to species of the subgenus *Nothonotus; E. juliae* is less atypical for *Nothonotus* than is *E. tippecanoe.*

8. Are the closest affinities of *E. exile* with species of *Oligocephalus,* or *Hololepis* and *Microperca*?

Collette (1962) noted the similarity between *E. exile* and species of *Hololepis,* citing as important characteristics the compressed body form, arched and incomplete lateral line, and pool habitat. The arching of the lateral line is intraspecifically variable in *E. exile,* but the lateral line is often abruptly arched upward anteriorly as it is in species of *Hololepis* and not in species of *Oligocephalus.*

Males of both *Hololepis* and *Microperca* develop breeding tubercles; species of *Oligocephalus* may or may not develop tubercles. The absence of tubercles in *E. exile* argues against a close relationship with species of *Hololepis* and *Microperca* but, because the absence of tuberles is plesiomorphous, is not an indication of relation to *Oligocephalus.* Tubercles have appeared independently within many darter groups (see Table 1 in Collette, 1965). *Hololepis* generally have a lower percentage of pored scales in the lateral row than do *Oligocephalus,* and *Hololepis* males generally have a smaller D2FL/QL ratio than do males of *Oligocephalus.* Contrasting these two characters (Fig. 11) shows a greater similarity between *E. exile* and species of *Hololepis* than it does between the primitive *E. serriferum* and other *Hololepis.*

Boleichthys is available as a subgeneric name for *E. exile* and predates *Hololepis* which therefore becomes a synonym of *Boleichthys.*

9. Is the separate subgeneric status of *Microperca* warranted?

Collette (1962) stated that species of *Microperca (E. proeliare, E. fonticola, E. microperca)* are the culmination of a phyletic line passing through *Hololepis.* That relationship is supported by phenograms (Figs. 3 & 5). Burr (1978) discussed the closeness of the two subgenera and noted the intermediacy of *E. saludae* and *E. collis* between the two subgenera.

It seems apparent that *E. saludae* and *E. collis* are more similar to species of *Microperca* than they are to some species of *Boleichthys,* and that *E. saludae, E. collis,* and *Microperca* share a common ancestor. *Boleichthys,* therefore, without *E. proeliare, E. fonticola,* and *E. microperca,* is not a monophyletic assemblage (sensu Hennig, 1966). It is necessary to synonymize *Microperca* under *Boleichthys* not only to have a monophyletic subgenus (as produced in Figs. 3 & 4) but also to remove the artificiality of grouping *E. saludae* and *E. collis* with distant relatives *(E. serriferum, E. fusiforme, E. exile)* and not with the more closely related *E.*

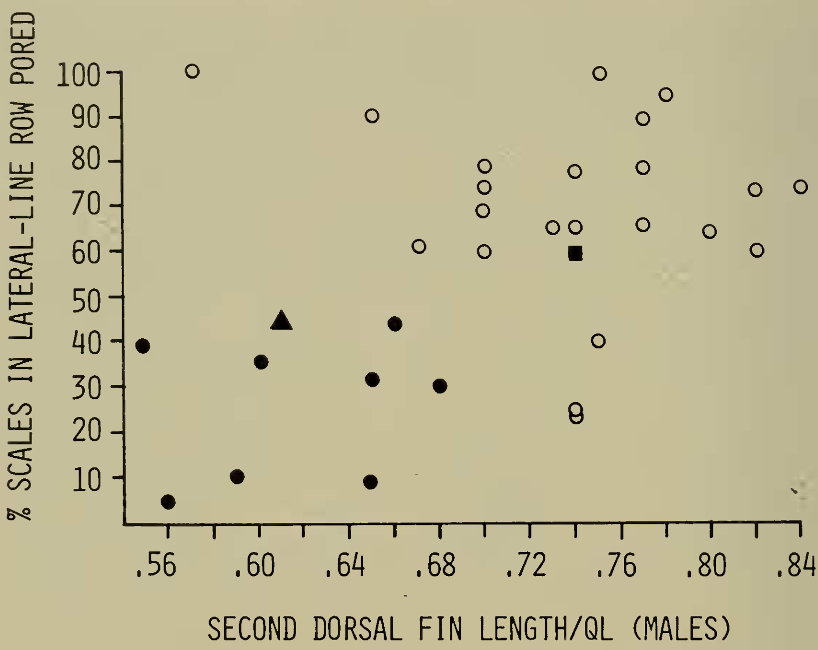

Fig. 11.—Scattergram of species of *Oligocephalus* sensu Bailey and Gosline (1955) (circles) and *Boleichthys* (dots, *E. serriferum* = square, *E. exile* = triangle) based on mean percentages of pored scales in lateral-line row and mean second dorsal fin lengths (relative to QL) of males.

proeliare. Synapomorphous characteristics of *Boleichthys* are the arched lateral line and adult females that average larger than males.

10. Is *Oligocephalus* polyphyletic?

In the preceding discussion *E. juliae* and *E. exile* were removed from *Oligocephalus*. The phenograms suggest that, even with these adjustments and removal of the *E. punctulatum* species group (Williams and Robison, 1980), *Oligocephalus* is an artificial assemblage of species. Further complicating consideration of the relationships of species assigned to *Oligocephalus* is the fact that *Villora*, as defined by Collette and Yerger (1962), and *Austroperca* are difficult to diagnose from *Oligocephalus*. Collette and Yerger (1962) commented on the morphological intermediacy of *E. okaloosae* between *E. (Villora) edwini* and *E. (Oligocephalus) swaini* and noted that they had not thoroughly compared *E. okaloosae* and *E. edwini* to *Oligocephalus*.

Bailey and Richards (1963) diagnosed *Oligocephalus* but the characteristics given were too variable to separate *Oligocephalus* from other subgenera of *Etheostoma*. In fact, no diagnostic characteristics unite the species referred to *Oligocephalus* by Bailey and Richards.

Some species groups among the species under consideration are suggested by the phenograms and are otherwise evident. These groups, proposed as subgenera, are shown in Table 4. The proposed new subgeneric classification is supported only in part by the phenograms but the subgenera can be diagnosed. Unless and until new data become available which allow more inclusive subgenera to be formed, it is not evident how further consolidation ought to proceed.

Color characteristics of darters are highly variable dimorphically, ontogenetically, and seasonally and consequently are difficult to verbalize with much precision. That, plus the fact that precise color characteristics are poorly known for many darters, prevented the utilization of color characteristics in the CLUSTER and WAGNER analyses. Recently acquired color slides of freshly preserved specimens of most species of darters enable the following analysis to be made. Further data on the colors of darters could help refine our ideas on their relationships.

Species of the *E. lepidum* group *(Oligocephalus)* except *E. grahami* and *E. pottsi* have in the first dorsal fin a blue (green in *E. lepidum* and *E. hopkinsi*) marginal band dorsad to a well-defined red band.[1] None of the other species under consideration (Table 4) has the blue-margin-over-red arrangement of bands. Apparently the only other species of *Etheostoma* with this characteristic are *E. stigmaeum, E. jessiae, E. coosae,* some undescribed species of *Nanostoma, E. exile, E. gracile,* and *E. zoniferum.* Generally, the bands in the last three species are smaller and less vivid than those in *Oligocephalus* (and in the last two species the dorsal band is more often gray than blue).

Another characteristic of all species in the reduced *Oligocephalus* (Table 4) is the presence of alternating dark and light vertical bars on the side of the body. Usually on females the dark bars are green, brown, or black and the light interspaces white to yellow; on large males the dark bars are usually blue to green and the interspaces are red to orange. The bars are typically best developed on the posterior half of the body. *E. mariae* and *E. parvipinne* sometimes have short vertical bars on the side but they never involve red and blue pigments. Breeding males of *E. fricksium* have red-orange bars alternating with green on the lower side.

In species of *Belophlox* and *Ozarka,* the first dorsal fin is margined or submargined (there may be a thin black margin along part or all of the fin) with red or orange. In *E. (Villora) edwini* the first

[1] In addition, clear bands, another blue band ventrad to the red band (e.g., in *E. asprigene* and some *E. spectabile*), or from top to bottom a blue-red-blue-red sequence (e.g., in *E. nuchale,* some *E. spectabile*) may be present. Bands are always most conspicuous in large males.

Table 4.—Characteristics of species formerly assigned to *Oligocephalus*, *Villora*, and *Austroperca*; + = modally present, — = modally absent. POM = preoperculomandibular, IO = infraorbital, ST = supratemporal.

	Distinctive coloration	Incomplete lateral line	Interrupted head canals IO	Interrupted head canals ST	Nine POM pores
Fuscatelum	No bright (red, blue, green or yellow)				
E. parvipinne	colors on body or fins	+	—	+	—
Belophlox	Red margin on first dorsal fin; side with broad				
E. fricksium	brown-black stripe (weakly developed in	—	—	—	—
E. mariae	*E. okaloosae*) and contrasting light lateral line	—	—	—	+
E. okaloosae		+,—	—	—	+
Villora	Male with red spots scattered over body and in				
E. edwini	2-4 rows in first dorsal fin	+	—	—	—
Ozarka					
E. trisella		—	—	—	—
E. punctulatum	Body mottled or speckled; male with bright	+	—	+	—
E. cragini	yellow-orange venter and margin or submargin	+	—	+	—
E. pallididorsum	on first dorsal fin	+	—	+	—
E. boschungi		+	—	+	—
Oligocephalus					
E. hopkinsi		+	—	—	—
E. whipplei		+	—	—	—
E. radiosum		+	—	—	—
E. ditrema	First dorsal fin with blue (green in *E. lepidum*	+	—	—	—
E. swaini	and *E. hopkinsi*) marginal band and well-defined	+	—	—	—
E. collettei	red band (except *E. grahami* and *E. pottsi*)	+	—	—	—
E. asprigene		+	—	—	—
E. caeruleum		+	—	—	—
E. australe		+	—	+,—	—
E. luteovinctum		+	+	—	—
E. lepidum		+	+	+	—
E. spectabile		+	+	—	—
E. nuchale		+	+	+	—
E. grahami		+	+	+	—
E. pottsi		+	+	+	—

dorsal fin is clear with two to four rows of discrete red spots. In *E. parvipinne,* for which the subgeneric name *Fuscatelum* is proposed, no bright colors in the fins or anywhere on the body are present.

Oligocephalus is further separable from *Belophlox* by modally having an incomplete lateral line and by not having a wide brown-black lateral stripe and contrasting light lateral line; from *Villora* by the relatively short and deep caudal peduncle; from *Ozarka* by the absence of the bright yellow-orange venter of the breeding male; and from *Fuscatelum* by the presence of bright colors.

E. grahami and *E. pottsi* appear to be specialized derivatives of, or early offshoots within, *Oligocephalus.* Unlike in other species of *Oligocephalus,* in *E. grahami* and *E. pottsi* the first dorsal fin is margined with red and has no blue band and vertical bars on the side of the body are only weakly developed. However, other characteristics and the general physiognomy agree with those of other *Oligocephalus* (female and young *E. lepidum* and *E. grahami* are often confused taxonomically) and leaving *E. grahami* and *E. pottsi* in *Oligocephalus* seems justified.

E. edwini and *E. okaloosae,* both referred to *Villora* by Collette and Yerger (1963), do not appear to be sufficiently related to be considered consubgenerics. In general body shape and coloration, *E. edwini* and *E. okaloosae* are quite dissimilar. The arching of the lateral line is much more pronounced in *E. edwini* (as noted by Collette and Yerger); in *E. okaloosae* the curve in the lateral line is nearly identical to that in some species of *Oligocephalus* (e.g., *E. swaini*). The short villous genital papilla characteristic of breeding females of both *E. edwini* and *E. okaloosae* appears to be structurally the same as in darters as diverse as *E. grahami* and *Percina sciera* and is not indicative of common ancestry.

E. australe, presumably referred previously to the monotypic subgenus *Austroperca* because it possesses only one anal spine, is except for not having two anal spines a typical *Oligocephalus* with red-over-blue bands in the first dorsal fin and strong vertical bars on the side of the body.

GENERA AND SUBGENERA

Genus *Percina* Haldeman

Diagnosis.—With modified (enlarged and strongly toothed) scales on breast of male; two anal spines; complete lateral line; uninterrupted head canals; opaque flesh; a distinctive electrophoretic mobility of the LDH B_4 isozyme (Page and Whitt, 1973b); mean body depth/standard length = 0.12-0.20.

Subgenera of *Percina* were diagnosed by Page (1974). Subsequent modifications in the diagnosis of the subgenus *Imostoma* were made by Etnier (1976) and Page (1976).

Genus *Ammocrypta* Jordan

Diagnosis.—Without modified (as in *Percina*) scales; one anal spine; complete lateral line; uninterrupted head canals; translucent flesh (when alive); without LDH B_4 isozyme mobility of *Percina;* body long and slender, mean body depth/standard length = 0.11-0.13.

The subgenus *Ammocrypta* was diagnosed by Williams (1975). *Crystallaria,* the other subgenus of *Ammocrypta* (s.l.) may be separated from *Ammocrypta* (s.s.) as follows.

Subgenus *Crystallaria* Jordan and Gilbert

Diagnosis.—Prevomer and palatine with teeth; premaxillary frenum present (narrow); caudal fin deeply forked; modally 12-15 dorsal spines, 13-14 dorsal rays, 12-15 anal rays, 45-48 vertebrae.

Genus *Etheostoma* Rafinesque

Diagnosis.—Without modified (as in *Percina*) scales; one or two anal spines; complete or incomplete lateral line; uninterrupted or interrupted head canals; opaque flesh (except translucent in *E. vitreum* which often has two anal spines); without LDH B_4 isozyme mobility of *Percina* (except in *E. cinereum* among species examined); mean body depth/standard length = 0.14-0.23.

Among the characters examined in the literature on darters and in the CLUSTER and WAGNER analyses (Appendix B), the following are the most useful in diagnosing subgenera of *Etheostoma.*

1. Lateral line arched or not arched upward anteriorly. In *Boleichthys* and *Villora* the lateral line characteristically is abruptly arched upward anteriorly, the apex of the arch being under the anterior half of the first dorsal fin. In some other subgenera, e.g. *Oligocephalus,* the line may be gently curved but not distinctly arched.
2. Lateral line complete or incomplete. Many species considered to have complete lateral lines occasionally have a few unpored scales in the lateral-line row; consequently, the lateral line arbitrarily is termed complete in any species in which 95% or more of the scales in the row are pored. Percentages of completeness are species means from Appendix C rounded to nearest 5%.
3. Infraorbital canal interrupted or uninterrupted.
4. Supratemporal canal interrupted or uninterrupted.
5. Number of preoperculomandibular pores.
6. Prevomer with or without teeth (data mainly from Richards, 1966).
7. Palatine with or without teeth (data mainly from Richards, 1966).
8. Number of branchiostegal rays.
9. Premaxillary frenum present or absent.

10. Number of anal spines.
11. Supraoccipital scaled (with scales) or unscaled (without scales).
12. Flesh opaque or translucent when alive.
13. Squamation of nape (fully scaled, partly scaled, unscaled).
14. Squamation of breast (fully scaled, partly scaled, unscaled).
15. Connection of branchiostegal membranes across isthmus (separate, narrowly joined, moderately joined, broadly joined).
16. Breeding tubercles present or absent on males (data mainly from Collette, 1965).
17. Branchiostegal membranes scaled or unscaled.
18. Depth of caudal peduncle relative to standard length. Means from Appendix C.
19. Number of anal rays.
20. Body depth relative to standard length. Means from Appendix C.
21. Interorbital width relative to head width. Means from Appendix C.
22. Snout length relative to body depth. Means from Appendix C.
23. Second dorsal fin length relative to distance from front of base of second dorsal fin to caudal base (of females). Means from Appendix C.
24. Pelvic fin length relative to standard length. Means from Appendix C.
25. Gape width relative to snout length. Means from Appendix C.
26. Adult males average larger or smaller than adult females.
27. Anus surrounded or not surrounded by villi.
28. Interpelvic fin width relative to pelvic fin base length.
29. Genital papilla of breeding male long and tubular or not long and tubular.
30. General shape of genital papilla of breeding female (illustrations and descriptions in Collette, 1962, 1965; Cole, 1967; Howell, 1968; Burr, 1978).
31. Site of egg deposition.
32. Particular color patterns in some subgenera. (The absence of those patterns in other subgenera is understood and not stated as such in each diagnosis.)

The combination of characteristics in the initial paragraph of each of the following subgeneric diagnoses separates that subgenus from all other subgenera of *Etheostoma*. The second paragraph of each diagnosis describes the states of characters used in the initial paragraphs of the diagnoses of other subgenera. Unless stated otherwise in the above list of characters or in the diagnoses, all characteristics are modal conditions.

The subgenera of *Etheostoma* are arranged in approximate primitive to advanced sequence (Table 1). Numerous phyletic lines are involved in the evolutionary history of the genus and the arrangement is subjective.

Psychromaster Jordan and Evermann

INCLUDED SPECIES.—*E. tuscumbia*. *Psychromaster*, as a subgenus of *Etheostoma* containing *E. tuscumbia* and *E. trisella*, was diagnosed by Bailey and Richards (1963).

DIAGNOSIS.—Supraoccipital region with scales; branchiostegal membranes with scales (variable intraspecifically); genital papilla of male long and tubular; one thick and stiff anal spine; lateral line not arched upward anteriorly; pelvic fins short (mean length/standard length = 0.16); gape wide in relation to snout length (mean width/snout length = 1.35).

Lateral line incomplete (25% scales in lateral-line row pored); infraorbital canal uninterrupted; supratemporal canal interrupted; modally 10 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; premaxillary frenum present; flesh opaque; nape and breast fully scaled; branchiostegal membranes separate; breeding tubercles absent; caudal peduncle deep (mean depth/standard length more than 0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding female short and conical; eggs attached to plants.

Litocara Bailey

INCLUDED SPECIES.—*E. sagitta*, *E. nianguae*.

DIAGNOSIS.—Modally 11 or 12 anal rays; base of caudal fin with two vertically aligned jet-black spots (often confluent in *E. sagitta* and breeding males).

Lateral line not arched upward anteriorly, incomplete to complete (90-100% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted; modally 10 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; premaxillary frenum present; modally two anal spines; supraoccipital unscaled; flesh opaque; nape fully scaled; breast unscaled; branchiostegal membranes separate to narrowly joined across isthmus; breeding tubercles present on body scales of male; branchiostegal membranes unscaled; caudal peduncle moderate in depth (mean depth/standard length = 0.08-0.11); mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of breeding female a short tube; eggs buried in substrate (known for *E. nianguae*).

Allohistium Bailey

INCLUDED SPECIES.—*E. cinereum*. *Allohistium* was diagnosed as a subgenus of *Etheostoma* by Bailey in Bailey and Gosline (1955).

DIAGNOSIS.—Snout long in relation to body depth (mean snout length/body depth = 0.54); palatine without teeth; modally six branchiostegal rays; nape and breast unscaled (or few scales posteriorly on nape); branchiostegal membranes separate to narrowly joined across isthmus; midlateral row of small black rectangles, upper sides with thin brown horizontal lines; first dorsal fin with red-brown margin.

Lateral line not arched upward anteriorly, complete (100% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted; modally 10 preoperculomandibular pores; prevomer with teeth; premaxillary frenum present; modally two anal spines, the first thick and stiff; supraoccipital unscaled; flesh opaque; nape and breast unscaled; breeding tubercles absent; branchiostegal membranes unscaled; caudal peduncle moderate in depth (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of breeding female unknown; egg deposition site unknown.

Etheostoma Rafinesque

INCLUDED SPECIES.—*E. blennioides, E. blennius, E. euzonum, E. histrio, E. inscriptum, E. kanawhae, E. osburni, E. rupestre, E. sellare, E. swannanoa, E. tetrazonum, E. thalassinum, E. vari-*

atum. *Etheostoma* was diagnosed as a subgenus including *E. zonale* by Richards (1966).

DIAGNOSIS.—Branchiostegal membranes broadly joined across the isthmus (narrowly joined in *E. sellare);* modally six branchiostegal rays and 10 preoperculomandibular pores (nine in *E. histrio* and *E. rupestre*); genital papilla of breeding female long and tubular (short and flat in *E. sellare*). *E. sellare* is apparently an early offshoot within subgenus *Etheostoma;* characteristics not strictly diagnostic for subgenus are indicative of relationship of *E. sellare* to certain species (*E. variatum* complex) of subgenus: back crossed by large and distinct dark-brown saddles which extend anteroventrally below lateral line; expansive pectoral fins.

Lateral line not arched anteriorly, complete (95-100% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted; prevomer and palatine with or without teeth; premaxillary frenum present or absent; modally two anal spines, the first thick and stiff; supraoccipital unscaled; flesh opaque; nape and breast fully scaled to unscaled; breeding tubercles absent, present on body scales of males, or present on body scales of males and females; branchiostegal membranes unscaled; caudal peduncle moderate in depth (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital moderate to wide (mean interorbital width/head width more than 0.16); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; genital papilla of breeding male not long and tubular; eggs attached to plants *(E. blennioides.)*

Nanostoma Putnam

INCLUDED SPECIES.—*E. zonale, E. atripinne, E. coosae, E. duryi, E. etnieri, E. simoterum,* and about 10 undescribed species. All included species except *E. zonale,* previously in *Etheostoma* (s.s.), were previously in *Ulocentra,* diagnosed by Bouchard (1977).

DIAGNOSIS.—Branchiostegal membranes broadly joined across isthmus, modally five branchiostegal rays and nine preoperculomandibular pores (six and 10, respectively, in *E. coosae*; 10 preoperculomandibular pores in *E. zonale*); genital papilla of breeding female long and tubular.

Lateral line not arched anteriorly, complete (95-100% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted; prevomer with or without teeth; palatine without teeth;

premaxillary frenum present or absent; modally two anal spines, the first thick and stiff; supraoccipital unscaled; flesh opaque; nape fully scaled; breast partly scaled to unscaled; breeding tubercles absent; branchiostegal membranes unscaled; caudal peduncle moderate in depth (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital moderate to wide (mean interorbital width/head width more than 0.16); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; genital papilla of breeding male not long and tubular; eggs attached to plants *(E. zonale)* or to sides of rocks (*E. atripinne, E. coosae,* and two undescribed species).

Doration Jordan

INCLUDED SPECIES.—*E. stigmaeum, E. jessiae. Doration* was diagnosed as a subgenus of *Etheostoma* by Cole (1967).

DIAGNOSIS.—First dorsal fin with blue marginal band and well-defined red band (bands conspicuous in large males); palatine without teeth; branchiostegal membranes narrowly joined across isthmus; genital papilla of breeding female long and tubular.

Lateral line not arched upward anteriorly, incomplete to complete (60-100% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted; modally 10 preoperculomandibular pores; prevomer with teeth; modally six branchiostegal rays; premaxillary frenum present or absent; modally two anal spines; supraoccipital unscaled; flesh opaque; nape fully to partly scaled; breast unscaled (sometimes partly scaled); breeding tubercles on body scales and anal and pelvic fins of males; branchiostegal membranes unscaled; caudal peduncle narrow (mean depth/standard length less than 0.08); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, length of second dorsal fin variable (mean fin length/distance from front of base of second dorsal fin to caudal base = 0.49-0.59); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular; eggs buried in substrate (known for *E. stigmaeum*).

Boleosoma DeKay

INCLUDED SPECIES.—*E. olmstedi, E. longimanum, E. nigrum, E. perlongum, E. podostemone. Boleosoma* was diagnosed as a subgenus of *Etheostoma* by Cole (1967).

DIAGNOSIS.—Female with broad, flat bifurcate genital papilla (Cole, 1967: fig. 3); eggs attached to underside of stone or log (known for four of five species) premaxillary frenum absent; interpelvic fin width/pelvic fin base length more than 0.675.

Lateral line not arched upward anteriorly, complete (95-100% scales in lateral-line row pored); infraorbital and supratemporal canals interrupted or uninterrupted; modally nine-11 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; modally one or two anal spines, thin and flexible; supraoccipital unscaled; flesh opaque; nape and breast fully scaled to unscaled; branchiostegal membranes narrowly to broadly joined across isthmus; breeding tubercles absent; branchiostegal membranes unscaled; caudal peduncle narrow to deep (mean depth/standard length less than 0.08 to more than 0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital moderate in width (mean interorbital width/head width between 0.16 and 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; genital papilla of breeding male not long and tubular.

Ioa Jordan and Brayton

INCLUDED SPECIES.—*E. vitreum.*

DIAGNOSIS.—Communal spawner, eggs attached to sides of rocks and logs; flesh translucent when alive; anus surrounded by villi; prevomer without teeth; snout long in relation to body depth (mean snout length/body depth = 0.56); interorbital narrow (mean interorbital width/head width = 0.15); body flattened (mean body depth/standard length = 0.14).

Lateral line not arched upward anteriorly, complete (95-100% scales in lateral-line row pored); infraorbital and supratemporal canal uninterrupted; modally 10 preoperculomandibular pores; palatine without teeth; modally six branchiostegal rays; premaxillary frenum absent; one or two anal spines, thin and flexible; supraoccipital unscaled; nape partly scaled; breast unscaled; branchiostegal membranes narrowly joined across isthmus; breeding tubercles present on pectoral and pelvic fins of males and females;

branchiostegal membranes unscaled; caudal peduncle narrow (mean depth/standard length less than 0.08); anal rays modally fewer than 11; in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; interpelvic fin width/pelvic fin base length more than 0.675; genital papilla of breeding male not long and tubular, of breeding female short and villous.

Vaillantia Jordan

INCLUDED SPECIES.—*E. chlorosomum*, *E. davisoni*. *Vaillantia* was diagnosed as a subgenus of *Etheostoma* by Cole (1967).

DIAGNOSIS.—Preorbital bars extend around snout as continuous black bridle; premaxillary frenum absent; palatine with teeth; incomplete lateral line (55-65% scales in lateral-line row pored); second dorsal fin short, in females mean fin length/distance from front of base of second dorsal fin to caudal base = 0.52.

Lateral line not arched upward anteriorly; infraorbital and supratemporal canals interrupted or uninterrupted; modally nine or 10 preoperculomandibular pores; prevomer with teeth, modally six branchiostegal rays; one or two anal spines, thin and flexible; supraoccipital unscaled; flesh opaque or semitranslucent when alive; nape partly scaled; breast partly scaled to unscaled; branchiostegal membranes narrowly to moderately joined across isthmus; breeding tubercles absent or present on anal and pelvic fins of male; branchiostegal membranes unscaled; caudal peduncle narrow (mean depth/standard length less than 0.08); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female villous; eggs attached to plants (known for *E. chlorosomum*).

Nothonotus Putnam

INCLUDED SPECIES.—*E. maculatum*, *E. acuticeps*, *E. aquali*, *E. bellum*, *E. camurum*, *E. chlorobranchium*, *E. jordani*, *E. juliae*, *E. microlepidum*, *E. moorei*, *E. rubrum*, *E. rufilineatum*, *E. tippecanoe*. *Nothonotus* was diagnosed as a subgenus of *Etheostoma* by Bailey (1959) and Zorach (1972).

DIAGNOSIS.—Sides of body with thin alternating dark and light lines (absent in *E. tippecanoe* and *E. jordani*); lateral line complete (95-100% scales in lateral-line row pored) (incomplete in *E. tippecanoe*); branchiostegal membranes separate to narrowly joined across isthmus (broadly joined in *E. juliae*); palatine with teeth; premaxillary frenum present; breeding tubercles absent; modally 10 preoperculomandibular pores; breast unscaled.

Lateral line not arched upward anteriorly; infraorbital and supratemporal canals uninterrupted; prevomer with teeth; modally six branchiostegal rays; modally two anal spines, the first thick and stiff; supraoccipital unscaled; flesh opaque; nape fully scaled (in *E. juliae*) to unscaled; branchiostegal membranes unscaled; caudal peduncle deep (mean depth/standard length more than 0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female short and conical or flat and broad but not bilobed; eggs buried in substrate (known for three species) or attached to underside of stone *(E. maculatum).*

Fuscatelum, new subgenus

TYPE SPECIES.—*Etheostoma parvipinne* Gilbert and Swain 1887.

INCLUDED SPECIES.—*E. parvipinne*. This species was formerly in the subgenus *Oligocephalus*. The name, *Fuscatelum* (dark-colored dart), emphasizes the absence of bright colors.

DIAGNOSIS.—No bright colors (red, blue, green or yellow) on body or fins; premaxillary frenum present; breeding tubercles present on anal fin of male.

Lateral line not arched upward anteriorly, incomplete (90% scales in lateral-line row pored); infraorbital canal uninterrupted; supratemporal canal interrupted; modally 10 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; modally two anal spines; supraoccipital unscaled; flesh opaque; nape fully scaled; breast fully to partly scaled; branchiostegal membranes moderately joined across isthmus; branchiostegal membranes unscaled; caudal peduncle deep (mean depth/standard length more than 0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female conical; egg deposition site unknown.

Belophlox Fowler

INCLUDED SPECIES.—*E. mariae, E. fricksium, E. okaloosae.* These species were formerly in the subgenera *Oligocephalus* and *Villora.*

DIAGNOSIS.—Lateral line complete or nearly complete (95-100% scales in lateral-line row pored); side of body with broad dark stripe (usually weakly developed in *E. okaloosae*) and contrasting light lateral line; first dorsal fin with red margin (or submargin); palatine with teeth.

Lateral line not arched upward anteriorly; infraorbital and supratemporal canals uninterrupted; modally nine or 10 preoperculomandibular pores; prevomer with teeth; modally six branchiostegal rays; premaxillary frenum present; modally two anal spines; supraoccipital unscaled; flesh opaque; nape partly to fully scaled; breast unscaled to fully scaled; branchiostegal membranes narrowly to broadly joined across isthmus; breeding tubercles absent or present on anal fin of male; branchiostegal membranes unscaled; caudal peduncle moderate (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus not surrounded by villi; narrow interpelvic width (mean width/pelvic fin base length = 0.27-0.46); genital papilla of breeding male not long and tubular, of female conical to tubular; eggs attached to plants *(E. okaloosae).*

Villora Hubbs and Cannon

INCLUDED SPECIES.—*E. edwini. Villora* as a subgenus of *Etheostoma* containing *E. edwini* and *E. okaloosae* was diagnosed by Collette and Yerger (1962).

DIAGNOSIS.—Lateral line distinctly arched upward anteriorly; adult males average larger than females; breeding male with two to four rows of red spots in first dorsal fin and red spots seattered over side of body; nape fully sealed.

Lateral line ineomplete (65% seales in lateral-line row pored); infraorbital and supratemporal eanals uninterrupted; modally 10 preopereulomandibular pores; prevomer and palatine with teeth; modally six branehiostegal rays; premaxillary frenum present; modally two anal spines, first thieker than seeond; supraoceipital unsealed; flesh opaque; breast partly to fully sealed; branehiostegal membranes separate to narrowly joined aeross isthmus; breeding tubereles absent; branehiostegal membranes unscaled; eaudal pedunele moderate (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, seeond dorsal fin not short (mean fin length/distanee from front of base of seeond dorsal fin to eaudal base more than 0.535); pelvie fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); anus not surrounded by villi; interpelvic fin width/pelvie fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female a short eone; eggs attached to plants.

Ozarka Williams and Robison

INCLUDED SPECIES.—*E. punctulatum*, *E. boschungi*, *E. cragini*, *E. pallididorsum*, *E. trisella*. These speeies were formerly in the subgenera *Oligocephalus* and *Psychromaster*.

DIAGNOSIS.—Bright yellow-orange venter and margin (or submargin) of first dorsal fin of breeding male; supratemporal canal interrupted (uninterrupted in *E. trisella*); side of body mottled or speckled, without vertical bars; breast unscaled.

Lateral line not arehed upward anteriorly, ineomplete (25-75% scales in lateral-line row pored) except in *E. trisella* which has eomplete lateral line (100% pored); infraorbital eanal uninterrupted; modally 10 preopereulomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; premaxillary frenum present; modally two anal spines (one in *E. trisella*); supraoceipital unsealed; flesh opaque; nape fully to partly sealed; branehiostegal membranes narrowly to moderately joined across isthmus; breeding tubercles present on anal and pelvie fins of male (absent in *E. trisella*); branchiostegal membranes unsealed; eaudal pedunele moderate to deep (mean depth/standard length more than 0.08); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult females average larger than males (?, known only for *E. pallididorsum*); anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female tubular; eggs laid on vegetation in seepage water (known for *E. boschungi* and *E. trisella*).

Oligocephalus Girard

INCLUDED SPECIES.—*E. lepidum, E. asprigene, E. australe, E. caeruleum, E. collettei, E. ditrema, E. grahami, E. hopkinsi, E. luteovinctum, E. nuchale, E. pottsi, E. radiosum, E. spectabile, E. swaini, E. whipplei. Oligocephalus,* as a subgenus of *Etheostoma* containing several species in addition to those above but not *E. australe,* was diagnosed by Bailey and Richards (1963).

DIAGNOSIS.—First dorsal fin with blue (green in *E. lepidum* and *E. hopkinsi*) marginal band and well-defined red band (bands conspicuous in large males), except in *E. grahami* and *E. pottsi*; prevomer and palatine with teeth; adult males average larger than females.

Lateral line not arched upward anteriorly, incomplete (40-90% scales in lateral-line row pored); infraorbital and supratemporal canals uninterrupted or interrupted; modally 10 preoperculomandibular pores; modally six branchiostegal rays; premaxillary frenum present; modally two anal spines (one in *E. australe*); supraoccipital unscaled; flesh opaque; nape and breast fully scaled to unscaled; branchiostegal membranes narrowly to moderately joined across isthmus; breeding tubercles absent or present on body scales and/or fins of male; branchiostegal membranes unscaled; caudal peduncle moderate to deep (mean depth/standard length more than 0.08); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of female tubular or conical; eggs buried in substrate (known for three species) or attached to plants (*E. lepidum* and *E. grahami*).

Catonotus Agassiz

INCLUDED SPECIES.—*E. flabellare, E. barbouri, E. kennicotti, E. neopterum, E. obeyense, E. olivaceum, E. smithi, E. squamiceps, E. striatulum, E. virgatum. Catonotus,* as a subgenus of *Etheostoma,* was diagnosed by Kuehne and Small (1971); that diagnosis was modified by Braasch and Page (1979).

DIAGNOSIS.—Genital papilla of female broad and flat, not bifurcate; eggs attached to underside of stone (known for nine species); supratemporal canal interrupted (except in occasional *E. flabellare*).

Lateral line not arched upward anteriorly, incomplete (10-75% scales in lateral-line row pored); infraorbital canal interrupted (uninterrupted in *E. neopterum* and *E. olivaceum*); modally nine or 10 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays; premaxillary frenum present; modally two anal spines; supraoccipital unscaled; flesh opaque; nape and breast fully scaled to unscaled; branchiostegal membranes separate to broadly joined across isthmus; breeding tubercles absent; branchiostegal membranes unscaled; caudal peduncle moderate to deep (mean depth/standard length more than 0.08); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22); snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); adult males average larger than females; anus surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular.

Boleichthys Girard

INCLUDED SPECIES.—*E. exile, E. collis, E. fonticola, E. fusiforme, E. gracile, E. microperca, E. proeliare, E. saludae, E. serriferum, E. zoniferum.* These species were formerly in the subgenera *Hololepis* (diagnosed as a subgenus of *Etheostoma* by Collette, 1962), *Microperca* (diagnosed as a subgenus of *Etheostoma* by Burr, 1978) and *Oligocephalus.*

DIAGNOSIS.—Lateral line distinctly arched upward anteriorly or absent (not always arched in *E. exile*); adult females average larger than males.

Lateral line incomplete (0-65% scales in lateral-line row pored); infraorbital canal interrupted or uninterrupted; supratemporal canal interrupted or uninterrupted; modally six-10 preoperculomandibular pores; prevomer and palatine with teeth; modally six branchiostegal rays (five in *E. microperca*); premaxillary frenum present; one or two anal spines (one in *E. proeliare* and *E. fonticola*); supraoccipital region unscaled to scaled; flesh opaque; nape fully scaled to unscaled; breast fully scaled to unscaled; branchiostegal membranes narrowly to moderately joined; breeding tubercles present on anal and pelvic fins of male (absent in *E. exile*); branchiostegal membranes unscaled; caudal peduncle moderate in depth (mean depth/standard length = 0.08-0.11); anal rays modally fewer than 11; mean body depth/standard length more than 0.145; interorbital wide (mean interorbital width/head width more than 0.22; snout not long in relation to body depth (mean snout length/body depth less than 0.53); in females, second dorsal fin not short (mean fin length/distance from front of base of second dorsal fin to caudal base more than 0.535); pelvic fins not short (mean fin length/standard length more than 0.16); gape not wide in relation to snout length (mean gape width/snout length less than 1.2); anus not surrounded by villi; interpelvic fin width/pelvic fin base length less than 0.675; genital papilla of breeding male not long and tubular, of breeding female conical, tubular or bilobed (but not flat and broad as in *Boleosoma*); eggs attached to plants (known for six of 10 species).

PHYLOGENY

The modified midventral scales of *Percina* are a derived characteristic setting apart all species in that genus from those in other darter genera. Although modified scales theoretically could have originated more than once among darters, the concurrence in distribution among darters of the modified scales and the "*Percina* mobility" of the LDH B_4 isozyme establishes beyond reasonable doubt that *Percina* is monophyletic (Page and Whitt, 1973b).

Ammocrypta and *Etheostoma* are not as easily diagnosed from one another as they are from *Percina* and the species from both genera could be included in one genus [rejecting the suggestion of Williams (1975) that *Ammocrypta* is derived from the subgenus *Imostoma* of *Percina*]. However, assuming that *Ammocrypta* diverged from *Etheostoma* prior to diversification within *Etheostoma* the recognition of *Ammocrypta* is satisfactory.

It is within *Etheostoma* that phylogenetic relationships are difficult to decipher. However, the subgeneric names presumably label the major avenues of diversification and certain characteristics provide some additional information on intersubgeneric relationships. Five major divisions can be recognized within *Etheostoma*: (1) *Boleichthys* (and perhaps *Villora*), (2) Psychromaster, (3) *Litocara*, (4) *Etheostoma, Nanostoma, Doration, Boleosoma, Ioa, Vail-*

lantia (and perhaps *Allohistium*), (5) *Nothonotus, Fuscatelum, Belophlox, Ozarka, Oligocephalus, Catonotus* (and perhaps *Villora* and *Allohistium*).

Boleichthys is set apart from all other subgenera by the combination of an arched lateral line (shared with *Villora*) and females which average larger than males. The serrae on the margin of the preopercle of *E. (Boleichthys) serriferum* and some individuals of *E. (B.) fusiforme, E. (B.) collis* (Collette, 1962) and *E. (B.) proeliare* (Burr, 1978) are essentially identical to the serrae of *Hadropterus*, the primitive subgenus of *Percina*, and of *Perca* and *Stizostedion*. Other species have crenulate margins on the preopercle but among *Etheostoma* only species of *Boleichthys* have serrae. The presence of this plesiomorphous characteristic suggests that *E. serriferum*, as the most primitive species of *Boleichthys*, is near the origin of an early phyletic line, and it is not likely that *Boleichthys* descended from any other extant group of *Etheostoma*. It is remarkable that *Boleichthys* contains what appears to be one of the most primitive species of *Etheostoma, serriferum*, and one considered to be the most highly evolved, *microperca* (Bailey and Gosline, 1955; Burr, 1978).

E. (Psychromaster) tuscumbia is the only species in *Etheostoma* in which scales are present on the branchiostegal membranes and in which the breeding male has a long tubular genital papilla.

E. (Litocara) nianguae and *sagitta* share a distinctive physiognomy (long head and snout, fusiform body) and color pattern (two vertically aligned jet-black spots on the caudal peduncle, large U-marks on the side of the body), and are the only species of *Etheostoma* modally to have more than 10 anal rays.

Boleosoma, Ioa and *Vaillantia* share a tendency toward reduction to one anal spine and have similar pigmentation. These three subgenera, and *Etheostoma, Nanostoma* and *Doration* share the tendency toward reduction and loss of the premaxillary frenum. They and *Allohistium* contain the only species of darters to have lost the palatine teeth.

The remaining subgenera (*Nothonotus, Fuscatelum, Belophlox, Ozarka, Oligocephalus, Catonotus* and perhaps *Villora*) are highly evolved. They may be interrelated to one another or they may be polyphyletic. Several of the advanced subgenera have breeding tubercles (Collette, 1965) and reductions in the lateralis system (Page, 1977); however, these characteristics have evolved independently among darters many times and impart little information about intersubgeneric relationships. Further elucidation of relationships among darters must await the accumulation of data beyond those presently available.

SUMMARY

In Bailey's classification of darters (Bailey and Gosline, 1955), three genera and 22 subgenera (eight in *Percina,* two in *Ammocrypta,* and 12 in *Etheostoma*) were recognized. Since 1955 one additional subgenus has been recognized in *Percina* (Page, 1974) and five additional subgenera have been recognized in *Etheostoma* (Collette and Yerger, 1962; Cole, 1967; Page and Whitt, 1973a; Williams and Robison, 1980) (Table 1).

In the present study, phenetic and cladistic procedures were used to examine relationships among 142 species of darters. Among the procedures used, UPGMA—correlation coefficient clustered the OTU's well (i.e. formed large clusters of small clusters) and gave results most congruent with the existing classification. Other methods were less satisfactory. Phenograms and cladograms were compared to the existing classification of darters and discordances were considered potential errors in classification and subjected to further analysis.

The three-genus classification of darters was supported. The following changes were made in the subgeneric classification of *Etheostoma.*

1. *Nanostoma* was recognized as a subgenus for *E. zonale.*
2. *Ulocentra* was synonymized with *Nanostoma.*
3. *E. juliae,* formerly in *Oligocephalus,* was transferred to *Nothonotus.*
4. *Villora* was reduced to a monotypic subgenus containing *E. edwini.*
5. *Fuscatelum,* new subgenus, was described for *E. parvipinne.*
6. *Belophlox* was recognized as a subgenus for *E. mariae, E. fricksium* and *E. okaloosae.*
7. *Austroperca* was synonymized with *Oligocephalus.*
8. *Boleichthys* was recognized as a subgenus for *E. exile.*
9. *Hololepis* and *Microperca* were synonymized with *Boleichthys.*

The three genera and all subgenera for which adequate diagnoses have not been published were diagnosed. Phylogenetic relationships among the genera of darters and among the subgenera of *Etheostoma* were discussed.

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APPENDIX A.—SPECIMENS EXAMINED

To obtain data for the numerical analysis 1,379 specimens representing 142 species were examined. The number of specimens per species ranged from 6 to 10 and averaged 9.7.

The following specimens were examined. Institution acronyms are identified in the acknowledgements. Numbers in parentheses are numbers of specimens examined. Locality data are available from the author.

Percina antesella: UT 91.471 (10); *P. aurantiaca:* UT 91.503 (4), 91.502 (6); *P. aurolineata:* TU 37676 (4), 40800 (2), 38197 (2); *P. burtoni:* TU 71983 (2), 72133 (1), 89496 (1), REJ—Copper Creek (6); *P. caprodes:*

INHS 75649 (10); *P. carbonaria:* TU 27454 (8); *P. copelandi:* INHS 75555 (10); *P. crassa:* INHS 75880 (6), NCMNH 3010 (4); *P. cymatotaenia:* INHS 75290 (10); *P. evides:* INHS 76728 (3), 76706 (7); *P. lenticula:* TU 60556 (2), 59560 (2), 58807 (3), 53715 (3); *P. macrocephala:* INHS 76641 (9), UMMZ 86386 (1); *P. macrolepida:* INHS 74774 (3), TU 64393 (2), 67567 (5); *P. maculata:* INHS 8541 (10); *P. nasuta:* OAM 4586 (2), 4843 (1), UTULSAC—Lee Creek (2), INHS 74993 (1), TU 72243 (4); *P. nigrofasciata:* INHS 74811 (2), 74800 (2), 76789 (3), 74816 (3); *P. notogramma:* USNM 107746 (10); *P. ouachitae:* INHS 76753 (8), 76766 (2), *P. oxyrhyncha:* UMMZ 17663 (6); *P. palmaris:* INHS 76305 (5), 76808 (2), 76806 (2), 76790 (1); *P. pantherina:* UTULSAC—Little River (6), Mountain Fork (1), Sixmile Creek (1), OAM 2559 (1); *P. peltata:* INHS 76809 (3), UMMZ 147594 (7); *P. phoxocephala:* INHS 26922 (10); *P. rex:* REJ—South Fork Roanoke R. (10); *P. roanoka:* INHS 75884 (10); *P. sciera:* INHS 26923 (10); *P. shumardi:* INHS 76783 (10); *P. squamata:* INHS 76768 (10); *P. tanasi:* INHS 75000 (5), TU 99120 (3); *P. uranidea:* TU 66011 (10); *P. (Alvordius)* species (Conasauga River): UT 91.501 (7), INHS 76807 (1), 76788 (2); *P. (Cottogaster)* species (Pearl River): TU 17732 (8); *P. (Odontopholis)* species (Barren River): INHS 76784 (10); *P. (Percina)* species (Conasauga River): TU 18369 (2), 69140 (5); *Ammocrypta asprella:* INHS 74792 (10); *A. beani:* UMMZ 170650 (10); *A. bifascia:* INHS 74773 (9); *A. clara:* INHS 13390 (10); *A. meridiana:* UMMZ 197722 (10); *A. pellucida:* INHS 17061 (4), 26929 (2), 16819 (2), 16794 (2); *A. vivax:* INHS 74946 (6), 74618 (4); *Etheostoma acuticeps:* INHS 75149 (9); *E. asprigene:* INHS 6116 (10); *E. atripinne:* INHS 74923 (10); *E. australe:* UMMZ 182378 (10); *E. barbouri:* INHS 74894 (7), 74906 (3); *E. bellum:* INHS 74865 (4), 74850 (3), 74878 (3); *E. blennioides:* INHS 74837 (10). *E. blennius:* UMMZ 168121 (10); *E. boschungi:* UMMZ 197692 (2), 197693 (2), 197691 (3); *E. caeruleum:* INHS 7205 (10); *E. camurum:* INHS 11816 (6), 11898 (2), 11815 (2); *E. chlorobranchium:* TU 96323 (10); *E. chlorosomum:* INHS 74818 (10); *E. cinereum:* UMMZ 171557 (5), 175061 (3), 171590 (2); *E. collettei:* INHS 76594 (10); *E. collis:* TU 71881 (7); *E. coosae:* UMMZ 190910 (10); *E. cragini:* INHS 74817 (10); *E. davisoni:* TU 83098 (10); *E. ditrema:* UMMZ 187501 (5), TU 32762 (3); *E. duryi:* INHS 77542 (10); *E. edwini:* INHS 74698 (8), 76375 (1); *E. etnieri:* TU 83149 (8); *E. euzonum:* UMMZ 124595 (8); *E. exile:* INHS 26934 (10); *E. flabellare:* INHS 22414 (10); *E. fonticola:* INHS 75562 (10); *E. fricksium:* TU 97596 (10); *E. fusiforme:* INHS 74269 (10); *E. gracile:* INHS 26933 (10); *E. grahami:* USNM 189023 (10); *E. histrio:* INHS 9617 (4), 16735 (6); *E. hopkinsi:* TU 39482 (10); *E. inscriptum:* INHS 74495 (10); *E. jessiae:* TU 34964 (10); *E. jordani:* INHS 74586 (10); *E. juliae:* INHS 74214 (4), 74228 (2), 74247 (4); *E. kanawhae:* UMMZ 169360 (10); *E. kennicotti:* INHS 1592 (10); *E. lepidum:* INHS 75687 (10); *E. longimanum:* USNM 162877 (10); *E. luteovinctum:* INHS 74559 (7), 74566 (2), 74579 (1); *E. maculatum:* INHS 74596 (10); *E. mariae:* INHS 75194 (9); *E. microlepidum:* UMMZ 168392 (10); *E. microperca:* INHS 4760 (10); *E. moorei:* UMMZ 181397 (10); *E. neopterum:* INHS 74278 (10); *E. nianguae:* INHS 74395 (4), 74397 (3), 74398 (2); *E. nigrum:* INHS 12873 (10); *E. nuchale:* USNM 217856 (10); *E. obeyense:* USNM 204345 (10); *E. okaloosae:* UMMZ 178859 (8), INHS 74688 (2); *E. olivaceum:* INHS 75879 (2), 75878 (8); *E. olmstedi:* INHS 74543 (10); *E. osburni:* UMMZ 165712 (9); *E. pallididorsum:* KU 6921 (10); *E. parvipinne:* INHS 74544 (10); *E. perlongum:* UMMZ 138476 (10); *E. podostemone:* USNM 162031 (10); *E. pottsi:* INHS 75300 (10); *E. proeliare:* INHS 1358 (10); *E. punctulatum:* UMMZ 137836 (10); *E. radiosum:* INHS 76580 (8), 76438 (2); *E. rubrum:* INHS 74325 (9); *E.*

rufilineatum: INHS 74309 (10); *E. rupestre:* INHS 76339 (10); *E. sagitta:* UL 5566 (10); *E. saludae:* USNM 196377 (10); *E. sellare:* USNM 212147 (10); *E. serriferum:* UMMZ 175866 (7), INHS 74361 (2); *E. simoterum:* INHS 74300 (10); *E. smithi:* INHS 75017 (10); *E. spectabile:* INHS 22556 (10); *E. squamiceps:* INHS 26936 (10); *E. stigmaeum:* INHS 74292 (10); *E. striatulum:* INHS 75037 (10); *E. swaini:* INHS 74378 (10); *E. swannanoa:* UMMZ 156073 (10); *E. tetrazonum:* INHS 76732 (10); *E. thalassinum:* INHS 74367 (2), 74735 (3), UMMZ 183619 (5); *E. tippecanoe:* INHS 74280 (10); *E. trisella:* TU 58963 (10); *E. tuscumbia:* USNM 217855 (9); *E. variatum:* UL 12459 (10); *E. virgatum:* NLU 10837 (10); *E. vitreum:* INHS 74355 (10); *E. whipplei:* UMMZ 177160 (9); *E. zonale:* INHS 76727 (10); *E. zoniferum:* TU 98971 (10); *E. (Catonotus)* species (Copper Creek, Scott Co., VA): TU 71976 (10); *E. (Doration)* species (Caney Fork): UMMZ 187465 (10); *E. (Nanostoma)* species 1 (Barren River): UMMZ 177622 (10); *E. (N.)* species 2 (Kentucky River): UMMZ 177854 (10); *E. (N.)* species 3 (Forked Deer River): UMMZ 177684 (8); *E. (N.)* species 4 (Sycamore Creek, Benton Co., TN): INHS 74279 (10); *E. (N.)* species 5 (Tallapoosa River): UMMZ 177758 (10); *E. (N.)* species 6 (Cumberland River): UMMZ 175042 (10); *E. (N.)* species 7 (Green River): UMMZ 177559 (10); *E. (N.)* species 8 (Black Warrior River): UAIC 3804 (10); *E. (N.)* species 9 (Cahaba River): UMMZ 168646 (10).

APPENDIX B.—CHARACTERS USED IN NUMERICAL ANALYSIS

Character 1.—Number of modified scales in single midbelly row from anus to pelvic fins (males).

Character 2.—Number of lateral scales (in row from opercle to end of hypural plate).

Character 3.—Percent of scales in lateral-line row that are pored.

Character 4.—Number of scale rows above lateral line (or above midlateral row of scales if line absent).

Character 5.—Number of scale rows below lateral line (or below midlateral row of scales if line absent).

Character 6.—Number of scale rows around caudal peduncle.

Character 7.—Number of pored scales on caudal fin.

Character 8.—Number of spines in first dorsal fin.

Character 9.—Number of rays in second dorsal fin.

Character 10.—Number of spines in anal fin.

Character 11.—Number of rays in anal fin.

Character 12.—Number of rays in pectoral fin.

Character 13.—Number of transverse scale rows (from anal fin origin anterodorsally to first dorsal fin).

Character 14.—Modal number of infraorbital pores.

Character 15.—Modal number of preoperculomandibular pores.

Character 16.—Modal number of branchiostegal rays.

Character 17.—Modal number of supratemporal pores.

Character 18.—Interpelvic fin width/pelvic fin base length (IP2/P2bL).

Character 19.—Head length/standard length (HL/SL).

Character 20.—Head width/standard length (HW/SL).

Character 21.—Body depth/standard length (BD/SL).

Character 22.—Caudal peduncle depth/standard length (CPD/SL).

Character 23.—Pectoral fin length/standard length (P1L/SL).

Character 24.—Predorsal length/standard length (PreDL/SL).

Character 25.—Snout (preorbital) length/body depth (SnL/BD).

Character 26.—Length of second dorsal fin base/length of first dorsal fin base (D2bL/D1bL).

Character 27.—Interorbital width/head width (IOW/HW).

Character 28.—Gape width/snout length (GW/SnL).

Character 29.—Body depth/anal fin length (males) (BD/AL).

Character 30.—Second dorsal fin length/distance from front of base of second dorsal fin to caudal base (males) (D2L/QL♂).

Character 31.—Second dorsal fin length/distance from front of base of second dorsal fin to caudal base (females) (D2L/QL♀).

Character 32.—Pelvic fin length/standard length (P2L/SL).

Character 33.—Caudal fin length/standard length (CFL/SL).

Character 34.—Flesh opaque or translucent when alive. 1 = opaque; 2 = translucent.

Character 35.—Pigment bar on cheek as in *E. virgatum* (see photo in Kuehne and Small, 1971). 1 = absent; 2 = present.

Character 36.—Breast squamation of males. 1 = fully scaled; 2 = reduced squamation, including scales embedded (neither fully scaled nor unscaled); 3 = unscaled.

Character 37.—Breast squamation of females. 1 = fully scaled; 2 = reduced squamation (neither fully scaled nor unscaled); 3 = unscaled.

Character 38.—Anterior belly squamation of males. 1 = area of belly immediately behind pelvic fins unscaled; 2 = area of belly immediately behind pelvic fins scaled.

Character 39.—Belly midline squamation of males. 1 = complete or incomplete rows of unmodified scales; 2 = scaleless strip(s) from pelvic fins to genital papilla; 3 = with a midbelly row of modified (enlarged and strongly toothed) scales on which the longest tooth is always less than 40% of the entire length of the modified scale; 4 = with a midbelly row of modified scales on which the teeth are sometimes longer than 40% of the entire length of the scales.

Character 40.—Belly midline squamation of females. 1 = fully scaled; 2 = variable, from almost fully scaled to a naked strip extending one-half distance from genital papilla to pelvic fins; 3 = variable, from almost unscaled to a naked strip extending one-half of distance from genital papilla to pelvic fins; 4 = unscaled from pelvic fins to genital papilla.

Character 41.—Uninterrupted interpelvic row of modified scales extending from approximately midpectoral area onto anterior part of belly (males). 1 = absent; 2 = present.

Character 42.—Conical snout projecting well beyond premaxilla. 1 = absent; 2 = present.

Character 43.—Premaxillary frenum. 1 = absent or extremely narrow; 2 = present and not extremely narrow.

Character 44.—Branchiostegal membrane connection. 1 = membranes not or only slightly joined; 2 = membranes narrowly to moderately joined; 3 = membranes broadly joined.

Character 45.—Lateral line. 1 = straight (complete or incomplete) or slightly arched; 2 = arched distinctly upward anteriorly.

Character 46.—Pelvic fins of breeding male. 1 = without large lateral flaps; 2 = with large lateral flaps.

Character 47.—Maximum size (total adult length). 1 = up to 55 mm; 2 = to 80 mm; 3 = to 105 mm; 4 = to 130 mm; 5 = to 155 mm; 6 = to 180 mm; 7 = over 180 mm.

Character 48.—Breeding tuberculation (including tubercular ridges). 1 = absent; 2 = present on males only; 3 = present on males and females (data mostly from Collette, 1965).

Character 49.—Cephalic canals. 1 = uninterrupted; 2 = supratemporal canal only interrupted; 3 = infraorbital canal only interrupted; 4 = both supratemporal and infraorbital canal interrupted.

Character 50.—Dentition. 1 = teeth present on prevomer and palatine; 2 = present on palatine and absent on prevomer; 3 = present on prevomer and absent on palatine; 4 = absent on both prevomer and palatine (data mostly from Richards, 1966).

Character 51.—Flesh over anterior half of maxillaries fused with skin over preorbitals. 1 = absent; 2 = present.

Character 52.—Anus surrounded by fleshy villi. 1 = absent; 2 = present.

Appendix C.—Character States Used In Numerical Analysis.

Species	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
P. aurantiaca	0.0	90.4	100.0	12.4	18.2	37.1	0.7	14.6	13.5	2.0	9.8	14.8	36.0
P. aurolineata	17.3	68.4	100.0	7.5	12.4	23.9	1.8	12.5	10.8	2.0	8.8	12.7	21.8
P. burtoni	35.2	88.7	100.0	13.7	18.8	35.2	0.0	16.1	14.5	2.0	11.1	14.4	34.8
P. caprodes	25.6	85.5	100.0	11.2	15.4	31.7	2.3	14.8	15.0	1.9	10.5	14.5	27.6
P. carbonaria	29.8	83.6	100.0	9.9	15.5	30.0	1.3	13.8	14.4	2.0	10.5	13.8	26.9
P. copelandi	9.5	52.6	100.0	4.8	6.8	16.7	0.1	9.4	11.1	2.0	8.2	13.4	13.8
P. crassa	6.3	49.6	100.0	5.4	7.8	18.1	0.0	11.5	11.7	2.0	8.5	13.8	15.8
P. cymatotaenia	0.0	70.6	100.0	7.4	10.6	23.8	0.0	13.1	12.6	2.0	10.5	12.1	19.7
P. evides	11.2	68.9	100.0	8.7	12.5	26.2	0.1	11.8	12.0	2.0	9.1	14.4	22.2
P. lenticula	21.0	82.2	100.0	10.3	16.2	31.9	2.6	13.1	13.0	2.0	9.1	14.2	28.7
P. macrocephala	16.0	84.8	100.0	8.7	14.6	28.1	0.0	13.8	13.0	2.0	9.6	13.9	25.4
P. macrolepida	25.0	86.0	99.9	7.8	11.6	28.7	0.1	14.7	14.2	2.0	8.7	13.1	20.8
P. maculata	7.8	64.1	100.0	8.4	11.3	24.6	0.0	13.5	11.8	2.0	9.3	13.2	19.9
P. nasuta	21.0	74.6	100.0	10.3	14.9	27.9	0.0	12.9	12.5	2.0	8.5	13.7	27.6
P. nigrofasciata	15.0	59.2	100.0	6.7	10.1	22.4	1.8	12.1	12.1	2.0	9.5	13.7	18.6
P. notogramma	7.4	54.6	100.0	6.5	10.0	21.4	0.2	12.6	11.8	2.0	9.0	14.4	17.5
P. oxyrhyncha	19.0	72.8	100.0	10.8	14.2	28.7	0.0	13.2	12.5	2.0	8.3	14.3	26.7
P. ouachitae	7.0	51.4	100.0	5.6	10.7	20.1	0.7	10.6	13.6	2.0	10.9	14.3	16.8
P. palmaris	11.0	66.0	100.0	7.4	10.6	23.9	0.1	13.1	11.3	2.0	8.7	13.9	20.0
P. pantherina	12.3	86.4	100.0	11.8	16.8	31.0	0.0	14.1	11.7	2.0	9.5	13.8	27.8
P. peltata	5.0	56.4	100.0	6.0	9.0	18.9	0.2	12.9	12.9	2.0	9.2	13.9	17.4
P. phoxocephala	21.5	66.6	100.0	9.3	14.1	25.7	0.1	11.6	11.9	2.0	9.3	14.4	23.3
P. rex	26.6	86.2	100.0	10.7	16.2	33.0	0.4	15.5	15.2	2.0	10.5	14.1	28.5
P. roanoka	8.5	47.7	100.0	5.0	6.4	16.1	0.2	10.8	11.1	2.0	8.4	14.0	12.9
P. sciera	15.2	63.4	100.0	7.6	13.2	23.1	1.6	12.3	11.4	2.0	8.5	14.1	20.2
P. shumardi	7.8	52.5	100.0	6.3	8.8	22.5	0.7	10.7	12.8	2.0	11.0	13.4	15.2
P. squamata	20.2	80.0	100.0	11.9	16.3	35.2	0.4	13.0	12.1	2.0	8.2	13.7	30.3
P. tanasi	13.4	53.0	100.0	6.1	9.1	22.1	0.3	10.1	14.6	2.0	11.4	13.9	17.0

P. uranidea	12.8	51.9	100.0	5.7	7.9	19.5	0.3	10.5	14.4	2.0	10.9	13.9	15.3
P. (Alvordius) sp.	17.2	69.4	100.0	6.7	11.4	25.2	0.0	13.2	9.8	2.0	8.0	13.7	19.7
P. (Cottogaster) sp.	7.5	54.0	100.0	4.9	9.4	21.1	0.0	11.0	12.6	2.0	8.5	13.6	16.6
P. (Imostoma) sp.	11.3	57.6	100.0	6.9	10.8	20.8	0.2	10.5	12.6	2.0	9.0	13.4	20.0
P. (Odontopholis) sp.	0.0	64.3	100.0	6.8	9.6	23.1	0.1	13.7	12.3	2.0	9.5	12.5	17.8
P. (Percina) sp.	34.4	92.1	100.0	12.6	19.1	37.4	0.4	16.6	14.9	2.0	10.3	14.4	33.4
A. asprella	0.0	88.9	100.0	7.3	11.6	26.5	2.7	12.7	13.3	1.0	13.6	16.4	21.8
A. beani	0.0	66.6	100.0	1.0	1.0	26.0	0.0	9.4	10.8	1.0	9.4	12.7	2.8
A. bifascia	0.0	68.7	100.0	0.7	1.3	32.9	0.2	9.0	10.4	1.0	9.2	13.3	3.1
A. clara	0.0	72.8	100.0	1.0	2.1	30.1	0.0	10.5	10.3	1.0	7.9	13.2	4.3
A. meridiana	0.0	73.1	100.0	5.9	9.7	29.1	0.0	10.7	9.7	1.0	8.9	13.2	18.1
A. pellucida	0.0	72.1	100.0	4.2	7.7	23.4	0.0	9.6	9.7	1.0	8.5	14.4	15.9
A. vivax	0.0	75.3	100.0	5.6	8.1	23.4	0.0	10.4	10.0	1.0	8.8	14.4	15.9
E. acuticeps	0.0	57.1	97.9	5.2	8.3	23.9	0.0	12.1	12.3	2.0	7.7	13.1	17.6
E. asprigene	0.0	49.1	78.2	4.8	8.2	21.0	0.0	10.2	13.0	2.1	7.9	13.3	15.0
E. atripinne	0.0	58.0	100.0	6.3	8.9	21.2	0.1	12.0	11.6	2.0	7.4	14.3	16.6
E. australe	0.0	62.1	70.9	6.8	9.4	27.9	0.0	12.0	10.7	1.0	7.3	11.1	17.5
E. barbouri	0.0	43.6	12.8	3.7	7.4	17.4	0.0	9.1	12.7	2.0	8.8	12.1	13.5
E. bellum	0.0	55.8	100.0	6.5	7.5	21.5	0.0	11.5	12.2	2.1	8.1	14.1	15.0
E. blennioides	0.0	60.5	99.2	6.2	9.0	22.4	0.0	12.6	13.5	2.0	8.7	14.0	17.1
E. blennius	0.0	42.0	98.6	4.2	6.3	17.7	0.0	11.3	11.5	2.0	8.1	15.8	12.6
E. boschungi	0.0	48.4	74.0	6.7	8.0	24.6	0.0	10.9	11.0	2.0	7.9	12.9	15.6
E. caeruleum	0.0	46.8	65.2	4.7	7.3	17.9	0.0	10.0	12.6	2.1	6.7	12.7	13.4
E. camurum	0.0	56.7	99.6	7.4	8.1	21.6	0.0	11.6	12.7	2.0	8.0	14.1	16.4
E. chlorobranchium	0.0	67.6	100.0	7.9	9.8	25.9	0.0	12.3	13.6	2.0	8.7	13.9	19.0
E. chlorosomum	0.0	54.1	56.2	4.7	6.2	17.2	0.0	9.7	10.4	1.0	7.9	13.1	12.4
E. cinereum	0.0	57.2	100.0	7.1	10.8	23.4	0.0	11.0	11.9	2.0	8.1	15.1	19.3
E. collettei	0.0	52.8	66.3	4.9	8.4	20.7	0.0	10.5	12.1	2.0	6.9	12.9	14.9
E. collis	0.0	47.0	31.7	2.3	7.9	19.9	0.0	9.9	11.0	1.0	7.6	11.7	11.9
E. coosae	0.0	51.1	98.6	5.2	8.3	19.7	0.1	9.9	11.9	2.0	7.0	13.5	15.1
E. cragini	0.0	48.4	23.9	6.7	7.1	23.3	0.0	9.3	11.6	2.0	7.1	11.6	14.6
E. davisoni	0.0	48.2	66.4	4.2	6.0	16.7	0.0	10.5	10.1	2.0	7.7	13.0	12.0

Appendix C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
E. ditrema	0.0	47.8	60.1	3.8	6.8	20.5	0.0	10.9	11.0	2.0	6.8	12.8	12.4
E. duryi	0.0	50.1	99.8	4.5	7.2	18.4	0.1	11.1	11.2	2.0	7.5	14.4	13.3
E. edwini	0.0	39.1	66.8	3.1	6.7	15.7	0.0	8.9	10.7	2.0	6.7	12.4	10.9
E. etnieri	0.0	50.0	98.6	5.1	6.8	19.8	0.0	10.9	11.0	2.0	6.9	14.5	13.1
E. euzonum	0.0	65.8	99.9	7.1	10.1	25.9	0.0	13.1	13.5	2.0	10.1	15.8	19.1
E. exile	0.0	55.4	45.5	4.4	7.8	19.7	0.0	9.0	11.3	2.0	7.8	12.5	14.2
E. flabellare	0.0	52.2	41.4	7.1	9.0	27.0	0.0	8.0	13.0	2.0	7.8	12.1	17.1
E. fonticola	0.0	32.8	8.2	4.0	5.5	17.3	0.0	6.7	10.7	1.0	6.4	10.1	10.8
E. fricksium	0.0	42.3	95.5	4.6	6.1	16.8	0.0	9.7	12.4	2.0	9.1	13.3	11.9
E. fusiforme	0.0	46.4	32.6	2.7	8.5	20.0	0.0	9.8	10.9	2.0	6.6	13.1	12.7
E. gracile	0.0	49.5	36.4	2.7	8.5	20.7	0.0	9.1	11.4	2.0	7.8	12.5	12.7
E. grahami	0.0	46.1	70.3	4.9	8.1	18.8	0.0	9.9	11.3	2.0	7.1	11.6	14.0
E. histrio	0.0	52.6	100.0	6.2	7.4	18.9	0.1	9.8	13.0	2.0	7.2	14.6	15.0
E. hopkinsi	0.0	47.3	77.8	3.9	6.9	19.0	0.0	10.5	12.1	2.0	8.1	12.7	12.3
E. inscriptum	0.0	49.5	100.0	4.8	6.6	18.1	0.0	10.0	11.3	2.0	8.0	13.4	13.2
E. jessiae	0.0	51.2	75.0	4.9	6.6	18.5	0.0	12.1	11.5	1.9	8.9	14.6	12.5
E. jordani	0.0	49.8	99.6	5.8	7.3	18.8	0.0	10.7	12.2	2.0	7.9	12.5	14.8
E. juliae	0.0	55.9	99.8	7.8	10.2	27.9	0.0	11.2	11.5	2.0	7.0	14.1	19.8
E. kanawhae	0.0	54.2	100.0	6.2	7.4	19.0	0.0	12.5	12.7	2.0	9.3	15.0	14.9
E. kennicotti	0.0	43.4	48.4	5.0	7.6	18.0	0.0	7.3	12.0	2.0	7.1	12.1	13.5
E. lepidum	0.0	54.8	61.7	5.9	8.5	22.5	0.0	9.5	11.2	2.0	6.9	11.9	15.1
E. longimanum	0.0	44.8	100.0	4.5	6.5	17.0	0.0	10.1	12.7	1.9	8.0	13.2	12.9
E. luteovinctum	0.0	54.9	69.0	5.6	9.0	23.0	0.0	9.6	12.7	2.0	7.4	12.8	16.1
E. maculatum	0.0	58.0	100.0	7.7	9.0	23.3	0.0	11.6	12.1	2.0	8.2	13.7	17.3
E. mariae	0.0	38.0	100.0	3.3	5.4	15.3	0.0	9.8	11.1	2.0	8.8	13.9	10.2
E. microlepidum	0.0	62.2	99.0	8.1	9.5	25.2	0.0	13.2	11.3	2.0	8.3	13.7	18.9
E. microperca	0.0	32.8	2.7	3.1	4.3	14.0	0.0	6.4	8.6	1.6	5.6	9.6	9.5
E. moorei	0.0	56.1	100.0	6.8	8.7	22.6	0.0	11.2	11.8	2.0	7.7	12.9	17.1

E. nianguae	0.0	77.6	100.0	11.3	13.7	27.6	0.0	10.8	13.7	2.0	12.0	14.9	25.4
E. nigrum	0.0	46.3	98.7	4.0	6.7	16.8	0.2	8.4	11.5	1.0	7.9	11.7	12.9
E. nuchale	0.0	37.8	42.3	4.0	5.9	15.6	0.0	9.4	10.6	2.0	7.1	11.9	11.0
E. obeyense	0.0	44.0	38.0	5.3	8.0	18.0	0.0	8.8	12.6	2.0	8.0	12.0	15.0
E. okaloosae	0.0	35.5	94.1	3.0	5.1	16.0	0.0	9.0	11.1	2.0	7.0	12.8	9.2
E. olivaceum	0.0	53.2	48.7	8.3	8.6	26.3	0.0	8.6	12.7	2.0	7.6	12.5	17.5
E. olmstedi	0.0	49.3	100.0	4.5	7.9	18.2	0.0	8.7	14.6	1.0	8.9	12.5	14.3
E. osburni	0.0	61.4	100.0	7.1	9.2	23.3	0.1	12.4	13.0	2.0	9.2	14.6	17.8
E. pallididorsum	0.0	48.9	24.5	7.9	7.0	23.3	0.0	9.4	11.2	2.0	7.6	11.1	14.8
E. parvipinne	0.0	54.2	91.9	6.5	8.6	23.4	0.0	9.5	10.6	2.0	8.5	15.0	16.5
E. perlongum	0.0	61.0	100.0	5.9	10.0	21.2	0.0	10.1	14.7	2.0	9.8	13.1	17.9
E. podostemone	0.0	39.2	100.0	4.0	6.0	15.7	0.0	9.6	13.0	2.0	7.3	12.2	11.9
E. pottsi	0.0	45.9	66.9	4.7	7.5	19.9	0.0	11.0	10.9	1.9	7.6	10.9	13.8
E. proeliare	0.0	35.8	10.3	2.2	5.5	15.2	0.0	8.1	10.4	1.7	6.0	10.1	9.2
E. punctulatum	0.0	66.6	66.7	10.4	11.6	28.2	0.0	10.5	14.0	2.0	8.1	12.7	21.8
E. radiosum	0.0	55.4	73.8	7.2	10.7	26.7	0.0	10.3	13.9	2.0	7.5	11.9	18.1
E. rubrum	0.0	50.8	99.3	7.0	7.3	20.2	0.0	10.9	11.3	2.0	7.8	13.4	15.2
E. rufilineatum	0.0	52.8	99.1	6.2	7.4	19.8	0.0	11.9	11.7	2.0	7.5	13.8	14.6
E. rupestre	0.0	57.8	100.0	6.2	9.4	21.5	0.1	11.5	11.8	2.0	7.0	14.5	17.2
E. sagitta	0.0	65.2	90.3	7.9	10.8	24.6	0.0	10.1	13.4	2.0	10.7	14.7	19.5
E. saludae	0.0	43.2	44.2	3.2	8.5	18.6	0.0	9.1	11.7	1.9	7.7	11.5	13.6
E. sellare	0.0	47.0	97.7	5.3	6.6	18.2	0.8	9.4	11.9	2.1	8.6	14.2	13.1
E. serriferum	0.0	57.3	60.0	3.8	11.2	25.7	0.0	11.0	12.8	2.0	6.8	12.0	15.8
E. simoterum	0.0	53.5	99.9	4.9	6.7	18.0	0.0	10.9	11.2	2.0	6.6	14.3	13.0
E. smithi	0.0	45.2	19.0	5.6	7.4	19.2	0.0	9.0	13.7	1.9	9.0	12.0	14.7
E. spectabile	0.0	48.3	62.1	5.1	7.8	18.6	0.0	9.5	12.9	2.0	7.0	11.6	14.4
E. squamiceps	0.0	50.4	66.9	5.8	7.2	18.6	0.0	8.3	12.8	2.0	7.4	10.9	14.2
E. stigmaeum	0.0	47.4	61.8	4.2	5.8	15.0	0.0	12.5	11.4	2.0	8.6	14.6	10.8
E. striatulum	0.0	44.4	26.4	5.0	7.9	18.7	0.0	8.3	13.5	2.0	9.0	11.9	14.1
E. swaini	0.0	39.0	90.9	4.2	6.7	18.1	0.0	10.4	11.1	2.0	6.6	12.0	12.2
E. swannanoa	0.0	51.6	99.9	4.2	6.4	18.8	0.0	11.8	12.5	1.9	8.1	16.0	12.8
E. tetrazonum	0.0	51.4	99.8	6.1	8.4	22.7	1.0	11.8	13.5	2.0	9.1	15.7	16.2

Appendix C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
E. thalassinum	0.0	44.5	100.0	4.2	6.1	16.3	0.0	9.7	11.5	2.0	8.5	13.6	12.2
E. tippecanoe	0.0	48.0	63.8	2.5	6.4	21.0	0.0	11.6	11.9	2.0	8.2	12.5	12.1
E. trisella	0.0	47.4	100.0	5.1	7.5	22.4	0.0	9.0	11.1	1.0	8.5	13.7	14.4
E. tuscumbia	0.0	47.2	23.1	7.2	9.0	22.3	0.0	9.8	12.1	1.0	8.3	11.8	16.9
E. variatum	0.0	53.3	99.6	7.0	8.1	22.4	0.1	12.3	13.1	2.0	9.3	14.6	16.5
E. virgatum	0.0	48.6	34.0	6.2	7.4	18.7	0.0	9.3	13.1	2.0	8.8	12.8	14.5
E. vitreum	0.0	57.8	99.8	6.7	7.8	20.0	0.0	8.4	13.3	2.0	9.2	12.9	16.3
E. whipplei	0.0	66.6	75.7	8.6	11.2	30.0	0.0	10.9	13.7	2.0	8.0	13.1	20.2
E. zonale	0.0	48.3	99.8	5.2	7.6	19.0	0.0	10.8	11.7	2.0	7.5	14.4	14.5
E. zoniferum	0.0	49.0	38.2	3.4	8.9	21.9	0.0	9.0	10.2	1.9	6.7	12.9	13.9
E. neopterum	0.0	48.1	74.2	5.9	7.4	21.1	0.0	8.9	11.0	2.0	6.6	11.7	14.5
E. (Catonotus) sp.	0.0	42.4	57.3	4.6	7.5	24.6	0.0	6.9	11.2	2.0	7.2	13.0	15.7
E. (Doration) sp.	0.0	46.1	96.9	3.9	5.5	17.4	0.0	11.1	11.0	2.0	7.8	14.8	10.7
E. (Nanostoma) sp. 1	0.0	46.0	99.1	4.1	7.5	17.1	0.0	11.0	11.6	2.0	7.4	13.9	13.3
E. (N.) sp. 2	0.0	49.9	96.9	5.2	7.8	19.2	0.0	10.8	10.7	2.0	6.9	14.7	15.1
E. (N.) sp. 3	0.0	39.6	99.4	3.9	6.3	17.1	0.0	10.6	11.4	2.0	7.5	13.9	12.0
E. (N.) sp. 4	0.0	47.0	98.3	4.5	6.8	18.3	0.0	10.3	10.7	2.0	6.9	13.4	12.5
E. (N.) sp. 5	0.0	49.3	99.0	4.8	7.4	19.3	0.0	10.3	11.1	2.0	7.3	14.3	13.7
E. (N.) sp. 6	0.0	47.7	99.6	5.2	7.3	17.9	0.0	10.8	11.1	2.0	7.0	14.8	14.0
E. (N.) sp. 7	0.0	40.2	99.8	3.8	5.7	15.2	0.1	10.8	10.9	1.9	7.2	14.1	10.8
E. (N.) sp. 8	0.0	50.1	96.8	4.8	7.4	18.8	0.0	10.3	10.9	2.0	6.9	14.2	13.7
E. (N.) sp. 9	0.0	47.7	97.9	5.0	7.0	18.4	0.0	10.8	11.5	2.0	7.8	13.7	13.7

APPENDIX C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	14	15	16	17	18	19	20	21	22	23	24	25	26
P. aurantiaca	8	10	6	3	0.953	0.245	0.121	0.160	0.098	0.188	0.305	0.436	0.549
P. aurolineata	8	10	6	3	0.668	0.238	0.114	0.162	0.080	0.194	0.311	0.345	0.488
P. burtoni	8	10	6	3	1.049	0.275	0.132	0.168	0.083	0.199	0.319	0.581	0.607
P. caprodes	8	10	6	3	1.042	0.263	0.133	0.168	0.083	0.192	0.323	0.516	0.704
P. carbonaria	8	10	6	3	0.809	0.256	0.126	0.169	0.092	0.223	0.321	0.479	0.671
P. copelandi	8	10	6	3	0.667	0.236	0.119	0.148	0.077	0.221	0.312	0.349	0.685
P. crassa	8	10	6	3	0.927	0.276	0.146	0.195	0.093	0.241	0.346	0.325	0.587
P. cymatotaenia	8	10	6	3	0.673	0.263	0.117	0.169	0.074	0.189	0.359	0.356	0.536
P. evides	8	10	6	3	0.600	0.265	0.137	0.174	0.087	0.221	0.328	0.410	0.616
P. lenticula	8	10	6	3	0.671	0.229	0.121	0.198	0.091	0.177	0.311	0.331	0.593
P. macrocephala	8	10	6	3	0.748	0.288	0.122	0.155	0.070	0.193	0.361	0.520	0.589
P. macrolepida	8	10	6	3	0.930	0.243	0.106	0.151	0.074	0.190	0.308	0.419	0.587
P. maculata	8	10	6	3	0.867	0.266	0.129	0.166	0.076	0.205	0.335	0.326	0.530
P. nasuta	8	10	6	3	0.688	0.301	0.104	0.148	0.083	0.200	0.372	0.608	0.562
P. nigrofasciata	8	10	6	3	0.589	0.256	0.127	0.178	0.084	0.220	0.326	0.359	0.568
P. notogramma	8	10	6	3	0.840	0.298	0.140	0.185	0.091	0.243	0.365	0.317	0.518
P. oxyrhyncha	8	10	6	3	0.725	0.302	0.114	0.155	0.093	0.216	0.356	0.536	0.565
P. ouachitae	8	10	6	3	0.936	0.260	0.144	0.185	0.070	0.224	0.338	0.372	0.734
P. palmaris	8	10	6	3	0.668	0.263	0.129	0.179	0.097	0.250	0.333	0.353	0.494
P. pantherina	8	10	6	3	0.928	0.266	0.113	0.136	0.072	0.200	0.336	0.487	0.475
P. peltata	8	10	6	3	0.911	0.266	0.127	0.155	0.073	0.238	0.347	0.398	0.591
P. phoxocephala	8	10	6	3	0.911	0.274	0.133	0.164	0.093	0.211	0.350	0.412	0.640
P. rex	8	10	6	3	0.778	0.267	0.127	0.159	0.084	0.221	0.319	0.561	0.667
P. roanoka	8	10	6	3	0.962	0.261	0.145	0.194	0.100	0.244	0.345	0.287	0.585
P. sciera	8	10	6	3	0.759	0.245	0.128	0.175	0.086	0.204	0.319	0.340	0.551
P. shumardi	8	10	6	3	0.753	0.271	0.154	0.172	0.092	0.233	0.339	0.407	0.868
P. squamata	8	10	6	3	0.909	0.285	0.103	0.139	0.089	0.192	0.347	0.551	0.556
P. tanasi	8	10	6	3	0.694	0.279	0.148	0.180	0.074	0.243	0.344	0.446	0.993

APPENDIX C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	14	15	16	17	18	19	20	21	22	23	24	25	26
P. uranidea	8	10	6	3	0.794	0.292	0.147	0.182	0.071	0.284	0.365	0.489	0.848
P. (Alvordius) sp.	8	10	6	3	0.799	0.257	0.108	0.119	0.065	0.198	0.334	0.469	0.427
P. (Cottogaster) sp.	8	10	6	3	0.959	0.252	0.125	0.154	0.079	0.234	0.313	0.402	0.660
P. (Imostoma) sp.	8	10	6	3	0.673	0.290	0.133	0.164	0.068	0.260	0.366	0.477	0.837
P. (Odontopholis) sp.	8	10	6	3	0.578	0.273	0.122	0.183	0.079	0.204	0.362	0.338	0.525
P. (Percina) sp.	8	10	6	3	1.130	0.261	0.129	0.156	0.074	0.201	0.327	0.602	0.644
A. asprella	8	10	6	3	0.789	0.253	0.126	0.127	0.051	0.212	0.330	0.679	0.821
A. beani	8	10	6	3	0.842	0.252	0.106	0.118	0.060	0.215	0.382	0.615	0.734
A. bifascia	8	10	6	3	0.761	0.260	0.116	0.109	0.055	0.240	0.391	0.780	0.806
A. clara	8	10	6	3	0.733	0.236	0.106	0.130	0.063	0.204	0.354	0.525	0.716
A. meridiana	8	10	6	3	0.763	0.239	0.106	0.128	0.068	0.218	0.368	0.503	0.617
A. pellucida	8	10	6	3	0.864	0.231	0.107	0.119	0.063	0.205	0.365	0.537	0.588
A. vivax	8	10	6	3	0.853	0.238	0.104	0.122	0.060	0.214	0.359	0.555	0.571
E. acuticeps	8	10	6	3	0.556	0.283	0.140	0.232	0.126	0.228	0.344	0.318	0.592
E. asprigene	8	10	6	3	0.282	0.284	0.149	0.205	0.108	0.231	0.340	0.325	0.677
E. atripinne	8	9	5	3	0.521	0.243	0.138	0.215	0.095	0.249	0.299	0.311	0.597
E. australe	8	10	6	4	0.321	0.298	0.138	0.199	0.101	0.263	0.363	0.333	0.575
E. barbouri	4	9	6	4	0.383	0.318	0.135	0.176	0.098	0.251	0.359	0.403	0.941
E. bellum	8	10	6	3	0.426	0.284	0.158	0.219	0.114	0.252	0.341	0.317	0.602
E. blennioides	8	10	6	3	0.729	0.241	0.150	0.186	0.095	0.261	0.306	0.365	0.697
E. blennius	8	10	6	3	0.638	0.245	0.152	0.200	0.090	0.340	0.333	0.394	0.715
E. boschungi	7	10	6	4	0.270	0.315	0.137	0.183	0.101	0.249	0.354	0.383	0.601
E. caeruleum	8	10	6	3	0.421	0.283	0.145	0.221	0.106	0.243	0.357	0.328	0.735
E. camurum	8	10	6	3	0.487	0.283	0.156	0.220	0.124	0.241	0.336	0.333	0.647
E. chlorobranchium	8	10	6	3	0.379	0.283	0.138	0.206	0.118	0.260	0.342	0.345	0.646
E. chlorosomum	5	10	6	4	0.493	0.273	0.123	0.150	0.078	0.250	0.331	0.427	0.657
E. cinereum	8	10	6	3	0.549	0.304	0.136	0.177	0.098	0.253	0.342	0.535	0.853
E. collettei	8	10	6	3	0.453	0.305	0.140	0.182	0.091	0.252	0.354	0.401	0.642

E. collis	4	9	6	4	0.279	0.263	0.116	0.176	0.090	0.220	0.318	0.286	0.774
E. coosae	7	9	6	3	0.388	0.256	0.140	0.210	0.102	0.272	0.320	0.299	0.764
E. cragini	7	10	6	4	0.155	0.305	0.144	0.181	0.104	0.252	0.361	0.348	0.789
E. davisoni	8	9	6	3	0.525	0.253	0.111	0.151	0.076	0.275	0.320	0.336	0.615
E. ditrema	8	10	6	4	0.276	0.284	0.131	0.187	0.096	0.217	0.341	0.277	0.659
E. duryi	8	9	5	3	0.502	0.251	0.137	0.193	0.093	0.290	0.327	0.333	0.656
E. edwini	8	10	6	3	0.448	0.288	0.127	0.189	0.094	0.255	0.330	0.300	0.664
E. etnieri	8	9	5	3	0.468	0.245	0.132	0.200	0.101	0.273	0.319	0.317	0.584
E. euzonum	8	10	6	3	0.658	0.275	0.139	0.178	0.080	0.290	0.346	0.500	0.697
E. exile	8	10	6	4	0.366	0.274	0.128	0.182	0.093	0.219	0.331	0.343	0.661
E. flabellare	6	10	6	4	0.605	0.287	0.150	0.193	0.131	0.226	0.348	0.311	1.055
E. fonticola	4	8	6	4	0.234	0.304	0.137	0.200	0.105	0.250	0.358	0.302	0.889
E. fricksium	8	10	6	3	0.267	0.284	0.124	0.183	0.102	0.256	0.337	0.293	0.751
E. fusiforme	4	9	6	3	0.468	0.268	0.114	0.172	0.101	0.226	0.322	0.321	0.653
E. gracile	8	10	6	3	0.316	0.283	0.134	0.181	0.092	0.238	0.340	0.300	0.675
E. grahami	6	10	6	4	0.466	0.284	0.145	0.213	0.115	0.231	0.348	0.312	0.643
E. histrio	8	10	6	3	0.736	0.247	0.151	0.192	0.089	0.348	0.322	0.390	0.805
E. hopkinsi	8	10	6	3	0.266	0.280	0.133	0.177	0.103	0.241	0.336	0.293	0.655
E. inscriptum	8	10	6	3	0.731	0.256	0.147	0.179	0.097	0.270	0.332	0.408	0.694
E. jessiae	8	10	6	3	0.354	0.285	0.123	0.160	0.074	0.266	0.346	0.520	0.639
E. jordani	8	10	6	3	0.603	0.293	0.139	0.198	0.111	0.263	0.358	0.346	0.634
E. juliae	8	10	6	4	0.651	0.289	0.150	0.232	0.124	0.276	0.353	0.335	0.610
E. kanawhae	8	10	6	3	0.682	0.256	0.147	0.188	0.097	0.331	0.326	0.416	0.648
E. kennicotti	5	10	6	4	0.446	0.300	0.137	0.170	0.104	0.251	0.345	0.360	0.798
E. lepidum	6	10	6	4	0.438	0.279	0.136	0.197	0.106	0.223	0.343	0.312	0.679
E. longimanum	8	10	6	3	0.867	0.248	0.151	0.187	0.103	0.327	0.321	0.358	0.846
E. luteovinctum	9	10	6	3	0.577	0.287	0.141	0.198	0.089	0.266	0.349	0.371	0.788
E. maculatum	8	10	6	3	0.566	0.281	0.119	0.198	0.121	0.228	0.353	0.345	0.559
E. mariae	7	9	6	3	0.456	0.280	0.138	0.205	0.103	0.273	0.340	0.291	0.739
E. microlepidum	8	10	6	3	0.502	0.286	0.126	0.196	0.120	0.243	0.353	0.319	0.506
E. microperca	4	6	5	4	0.135	0.286	0.136	0.199	0.105	0.266	0.353	0.271	0.880
E. moorei	8	10	6	3	0.445	0.285	0.135	0.212	0.128	0.240	0.343	0.299	0.570

Appendix C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	14	15	16	17	18	19	20	21	22	23	24	25	26
E. nianguae	8	10	6	3	0.391	0.293	0.122	0.160	0.088	0.198	0.356	0.402	0.766
E. nigrum	6	9	6	3	0.752	0.262	0.132	0.165	0.085	0.242	0.322	0.375	0.859
E. nuchale	8	10	6	4	0.491	0.289	0.139	0.197	0.104	0.248	0.351	0.320	0.667
E. obeyense	6	10	6	4	0.476	0.303	0.143	0.174	0.095	0.238	0.360	0.400	0.887
E. okaloosae	8	9	6	3	0.358	0.278	0.127	0.198	0.110	0.270	0.349	0.290	0.790
E. olivaceum	8	10	6	4	0.478	0.292	0.141	0.199	0.112	0.234	0.369	0.324	0.919
E. olmstedi	8	10	6	3	0.864	0.275	0.148	0.175	0.088	0.247	0.333	0.439	1.155
E. osburni	8	10	6	3	0.608	0.276	0.145	0.174	0.096	0.292	0.342	0.479	0.639
E. pallididorsum	7	10	6	4	0.395	0.301	0.144	0.185	0.116	0.236	0.351	0.349	0.685
E. parvipinne	8	10	6	4	0.580	0.280	0.142	0.178	0.121	0.221	0.359	0.311	0.654
E. perlongum	8	10	6	3	0.686	0.234	0.122	0.146	0.072	0.254	0.301	0.439	1.070
E. podostemone	8	9	6	3	0.983	0.240	0.158	0.170	0.118	0.304	0.304	0.356	0.904
E. pottsi	8	10	6	4	0.412	0.315	0.143	0.212	0.116	0.237	0.372	0.306	0.685
E. proeliare	4	8	6	4	0.427	0.282	0.130	0.187	0.094	0.254	0.331	0.313	0.810
E. punctulatum	8	10	6	4	0.305	0.310	0.138	0.198	0.108	0.250	0.345	0.369	0.778
E. radiosum	8	10	6	3	0.382	0.310	0.130	0.190	0.103	0.242	0.357	0.359	0.795
E. rubrum	8	10	6	3	0.460	0.283	0.137	0.220	0.119	0.245	0.348	0.290	0.594
E. rufilineatum	8	10	6	3	0.535	0.287	0.138	0.213	0.118	0.248	0.350	0.354	0.594
E. rupestre	7	9	6	3	0.832	0.245	0.151	0.172	0.093	0.313	0.321	0.460	0.646
E. sagitta	8	10	6	3	0.478	0.301	0.128	0.162	0.092	0.235	0.362	0.396	0.765
E. saludae	5	9	6	3	0.605	0.271	0.136	0.190	0.093	0.231	0.332	0.271	0.754
E. sellare	8	10	6	3	0.765	0.266	0.164	0.181	0.097	0.311	0.336	0.392	0.743
E. serriferum	6	9	6	3	0.317	0.261	0.111	0.177	0.105	0.269	0.301	0.263	0.844
E. simoterum	8	9	5	3	0.607	0.245	0.141	0.219	0.094	0.261	0.317	0.302	0.647
E. smithi	4	10	6	4	0.418	0.300	0.140	0.175	0.096	0.251	0.342	0.393	1.193
E. spectabile	7	10	6	3	0.378	0.304	0.152	0.205	0.102	0.268	0.346	0.348	0.840
E. squamiceps	8	10	6	4	0.478	0.291	0.155	0.181	0.110	0.229	0.350	0.345	1.045
E. stigmaeum	8	10	6	3	0.384	0.262	0.136	0.172	0.079	0.263	0.319	0.426	0.494

E. striatulum	4	10	6	4	0.458	0.321	0.141	0.176	0.095	0.262	0.368	0.383	1.102
E. swaini	8	10	6	3	0.463	0.300	0.152	0.208	0.112	0.264	0.348	0.325	0.639
E. swannanoa	8	10	6	3	0.686	0.243	0.144	0.184	0.096	0.309	0.322	0.390	0.661
E. tetrazonum	8	10	6	3	0.632	0.288	0.157	0.204	0.093	0.321	0.346	0.416	0.685
E. thalassinum	8	10	6	3	0.649	0.269	0.157	0.205	0.106	0.291	0.340	0.357	0.706
E. tippecanoe	7	10	6	3	0.427	0.277	0.130	0.201	0.117	0.269	0.345	0.350	0.621
E. trisella	8	10	6	3	0.386	0.309	0.128	0.165	0.091	0.267	0.361	0.387	0.683
E. tuscumbia	8	10	6	4	0.521	0.286	0.153	0.204	0.116	0.208	0.326	0.293	0.882
E. variatum	8	10	6	3	0.849	0.280	0.163	0.211	0.100	0.316	0.341	0.373	0.637
E. virgatum	6	10	6	4	0.439	0.315	0.129	0.170	0.096	0.246	0.365	0.409	0.930
E. vitreum	8	10	6	3	0.888	0.242	0.147	0.144	0.073	0.303	0.350	0.563	1.114
E. whipplei	8	10	6	3	0.490	0.299	0.142	0.192	0.099	0.222	0.353	0.354	0.680
E. zonale	7	10	5	3	0.447	0.247	0.135	0.201	0.101	0.280	0.331	0.302	0.620
E. zoniferum	6	10	6	4	0.284	0.280	0.122	0.168	0.101	0.217	0.325	0.311	0.643
E. neopterum	8	10	6	4	0.486	0.301	0.153	0.192	0.120	0.243	0.360	0.317	0.848
E. (Catonotus) sp.	6	10	6	4	0.493	0.314	0.136	0.176	0.111	0.268	0.374	0.404	0.778
E. (Doration) sp.	8	10	6	3	0.615	0.267	0.126	0.154	0.072	0.255	0.332	0.516	0.577
E. (Nanostoma) sp. 1	8	9	5	3	0.486	0.237	0.134	0.213	0.096	0.287	0.313	0.280	0.634
E. (N.) sp. 2	8	10	5	3	0.546	0.238	0.126	0.168	0.091	0.276	0.312	0.326	0.587
E. (N.) sp. 3	7	9	5	3	0.278	0.249	0.127	0.184	0.092	0.266	0.320	0.284	0.673
E. (N.) sp. 4	8	9	5	3	0.424	0.255	0.129	0.202	0.090	0.260	0.330	0.269	0.634
E. (N.) sp. 5	8	9	5	3	0.424	0.248	0.136	0.190	0.099	0.288	0.327	0.337	0.659
E. (N.) sp. 6	8	9	5	3	0.447	0.242	0.135	0.211	0.096	0.265	0.321	0.273	0.618
E. (N.) sp. 7	8	9	5	3	0.512	0.239	0.141	0.211	0.094	0.283	0.310	0.283	0.594
E. (N.) sp. 8	8	9	5	3	0.477	0.260	0.135	0.192	0.101	0.275	0.329	0.333	0.622
E. (N.) sp. 9	8	9	5	3	0.445	0.245	0.136	0.185	0.093	0.266	0.327	0.326	0.661

Appendix C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	27	28	29	30	31	32	33	34	35	36	37	38	39
P. aurantiaca	0.404	0.797	0.661	0.665	0.627	0.101	0.153	1	1	2	2	2	1
P. aurolineata	0.336	0.714	0.603	0.642	0.585	0.169	0.153	1	1	1	1	2	3
P. burtoni	0.491	0.635	0.642	0.789	0.690	0.178	0.162	1	1	2	3	1	3
P. caprodes	0.458	0.641	0.666	0.778	0.727	0.184	0.173	1	1	3	3	1	3
P. carbonaria	0.420	0.557	0.602	0.818	0.672	0.206	0.178	1	1	3	3	1	3
P. copelandi	0.315	0.993	0.588	0.626	0.543	0.179	0.190	1	1	3	3	1	3
P. crassa	0.317	0.953	0.769	0.709	0.690	0.205	0.191	1	1	3	3	1	4
P. cymatotaenia	0.390	0.754	0.640	0.708	0.576	0.188	0.163	1	1	1	1	2	1
P. evides	0.326	0.971	0.650	0.728	0.655	0.189	0.177	1	1	3	3	1	3
P. lenticula	0.454	0.730	0.796	0.682	0.653	0.174	0.185	1	1	1	1	2	3
P. macrocephala	0.305	0.683	0.687	0.690	0.595	0.157	0.148	1	1	3	3	1	3
P. macrolepida	0.435	0.609	0.693	0.685	0.634	0.178	0.180	1	1	2	2	1	3
P. maculata	0.348	1.133	0.675	0.652	0.598	0.184	0.175	1	1	3	3	1	4
P. nasuta	0.280	0.473	0.870	0.669	0.628	0.176	0.161	1	1	3	3	1	3
P. nigrofasciata	0.354	0.806	0.685	0.692	0.652	0.190	0.167	1	1	1	2	1	3
P. notogramma	0.285	0.990	0.729	0.768	0.621	0.217	0.200	1	1	3	3	1	3
P. oxyrhyncha	0.271	0.484	0.696	0.633	0.608	0.195	0.173	1	1	2	2	2	3
P. ouachitae	0.240	1.036	0.480	0.664	0.670	0.189	......	1	1	3	3	1	3
P. palmaris	0.282	0.795	0.620	0.716	0.684	0.216	0.176	1	1	3	3	1,2	3
P. pantherina	0.285	0.912	0.600	0.591	0.531	0.176	0.170	1	1	3	3	1	3
P. peltata	0.339	0.937	0.618	0.625	0.637	0.206	0.197	1	1	3	3	1	4
P. phoxocephala	0.293	0.932	0.722	0.623	0.650	0.180	0.170	1	1	3	3	2	3
P. rex	0.462	0.594	0.558	0.654	0.738	0.198	0.176	1	1	3	3	1	3
P. roanoka	0.289	1.299	0.765	0.664	0.657	0.211	0.185	1	1	3	3	1	3
P. sciera	0.390	1.103	0.713	0.661	0.615	0.183	0.175	1	1	3	3	2	3
P. shumardi	0.268	0.946	0.551	0.679	0.657	0.208	0.195	1	1	3	3	1	3
P. squamata	0.341	0.546	0.691	0.595	0.585	0.181	0.157	1	1	2	2	2	3
P. tanasi	0.327	0.696	0.534	0.823	0.717	0.191	0.186	1	1	2	2	1	3

P. uranidea	0.291	0.782	0.465	0.900	0.740	0.234	0.197	1	1	2	2	1	3
P. (Alvordius) sp.	0.359	0.753	0.560	0.550	0.493	0.159	0.168	1	1	3	3	2	3
P. (Cottogaster) sp.	0.302	0.917	0.586	0.683	0.596	0.191	0.203	1	1	3	3	1	3
P. (Imostoma) sp.	0.244	0.579	0.457	0.775	0.691	0.207	0.161	1	1	3	3	1	3
P. (Odontopholis) sp.	0.368	0.802	0.733	0.713	0.601	0.192	0.175	1	1	1	1	2	1
P. (Percina) sp.	0.492	0.456	0.587	0.763	0.704	0.178	0.159	1	1	3	3	2	3
A. asprella	0.251	0.601	0.418	0.638	0.545	0.196	0.162	2	1	3	3	1	2
A. beani	0.292	0.655	0.478	0.619	0.556	0.174	0.167	2	1	3	3	1	2
A. bifascia	0.305	0.678	0.423	0.663	0.595	0.182	0.175	2	1	3	3	1	2
A. clara	0.361	0.530	0.611	0.530	0.543	0.169	0.171	2	1	3	3	1	2
A. meridiana	0.314	0.589	0.629	0.524	0.487	0.197	0.172	1	1	3	3	1	2
A. pellucida	0.417	0.647	0.544	0.561	0.501	0.187	0.164	2	1	3	3	1	2
A. vivax	0.284	0.640	0.547	0.523	0.505	0.191	0.157	2	1	3	3	1	2
E. acuticeps	0.294	0.569	0.920	0.815	0.772	0.184	0.167	1	1	3	3	2	1
E. asprigene	0.332	0.910	0.805	0.768	0.742	0.207	0.212	1	1	3	3	2	1
E. atripinne	0.353	0.821	0.823	0.764	0.657	0.206	0.201	1	1	3	3	2	1
E. australe	0.345	0.848	0.829	0.666	0.619	0.189	0.197	1	1	3	3	1	1
E. barbouri	0.354	0.846	0.544	0.930	0.744	0.207	0.226	1	2	3	3	1	1
E. bellum	0.301	0.942	0.858	0.768	0.765	0.211	0.185	1	1	3	3	2	1
E. blennioides	0.204	0.839	0.796	0.684	0.698	0.224	0.184	1	1	3	3	2	1
E. blennius	0.212	0.502	0.819	0.675	0.631	0.237	0.199	1	1	3	3	2	1
E. boschungi	0.393	1.012	0.791	0.701	0.663	0.213	0.214	1	1	3	3	2	1
E. caeruleum	0.304	0.852	0.920	0.796	0.755	0.207	0.183	1	1	3	3	2	1
E. camurum	0.301	0.975	0.887	0.794	0.754	0.196	0.184	1	1	3	3	2	1
E. chlorobranchium	0.352	0.908	0.798	0.742	0.731	0.207	0.197	1	1	3	3	2	1
E. chlorosomum	0.346	0.894	0.732	0.543	0.531	0.212	0.215	1	1	2	2	1	1
E. cinereum	0.320	0.578	0.767	0.724	0.674	0.228	0.195	1	1	3	3	2	1
E. collettei	0.314	0.943	0.827	0.734	0.721	0.196	0.196	1	1	3	3	2	1
E. collis	0.385	1.062	0.700	0.679	0.645	0.195	0.221	1	1	3	3	1	1
E. coosae	0.302	0.732	0.784	0.736	0.655	0.208	0.206	1	1	3	3	2	1
E. cragini	0.413	1.126	0.701	0.738	0.714	0.205	0.254	1	1	3	3	1	1
E. davisoni	0.303	1.013	0.733	0.570	0.519	0.195	0.208	1	1	3	3	1	1

APPENDIX C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	27	28	29	30	31	32	33	34	35	36	37	38	39
E. ditrema	0.356	1.083	0.792	0.688	0.594	0.195	0.219	1	1	2	2	2	1
E. duryi	0.308	0.721	0.708	0.793	0.643	0.226	0.205	1	1	3	3	2	1
E. edwini	0.419	0.979	0.724	0.696	0.650	0.202	0.225	1	1	1	1	2	1
E. etnieri	0.341	0.767	0.811	0.688	0.590	0.222	0.192	1	1	2	2	2	1
E. euzonum	0.245	0.513	0.704	0.740	0.711	0.236	0.192	1	1	2	2	2	1
E. exile	0.388	0.898	0.746	0.605	0.587	0.194	0.202	1	1	3	3	2	1
E. flabellare	0.330	0.963	0.738	0.848	0.818	0.164	0.201	1	1	3	3	2	1
E. fricksium	0.422	0.949	0.639	0.787	0.754	0.199	0.205	1	1	3	3	1	1
E. fusiforme	0.401	1.111	0.715	0.654	0.631	0.195	0.239	1	1	1	1	2	1
E. gracile	0.381	0.991	0.763	0.603	0.569	0.206	0.204	1	1	3	3	1	1
E. grahami	0.401	0.954	0.940	0.704	0.647	0.192	0.194	1	1	3	3	2	1
E. histrio	0.283	0.723	0.725	0.743	0.763	0.260	0.214	1	1	3	3	1	1
E. hopkinsi	0.303	1.061	0.737	0.737	0.720	0.196	0.199	1	1	3	3	1	1
E. inscriptum	0.270	0.820	0.768	0.652	0.639	0.162	0.197	1	1	3	3	1	1
E. jessiae	0.247	0.732	0.719	0.670	0.591	0.206	0.196	1	1	3	3	2	1
E. jordani	0.288	0.814	0.746	0.794	0.745	0.201	0.190	1	1	3	3	2	1
E. juliae	0.265	0.743	0.856	0.848	0.776	0.210	0.205	1	1	3	3	2	1
E. kanawhae	0.256	0.722	0.716	0.801	0.702	0.223	0.202	1	1	2	2	2	1
E. kennicotti	0.300	0.990	0.642	0.803	0.770	0.204	0.224	1	1	3	3	1	1
E. lepidum	0.420	0.975	0.849	0.666	0.617	0.196	0.199	1	1	2	3	2	1
E. longimanum	0.207	0.820	0.667	0.907	0.720	0.240	0.227	1	1	3	3	1	1
E. luteovinctum	0.288	0.860	0.832	0.691	0.629	0.217	0.228	1	1	2	2	2	1
E. maculatum	0.297	0.669	0.792	0.826	0.784	0.183	0.171	1	1	3	3	2	1
E. mariae	0.389	1.006	0.695	0.774	0.741	0.206	0.214	1	1	2	2	1	1
E. microlepidum	0.361	0.777	0.776	0.772	0.742	0.203	0.176	1	1	3	3	2	1
E. microperca	0.490	0.813	0.795	0.557	0.549	0.313	0.261	1	1	3	3	1	1
E. moorei	0.301	0.865	0.831	0.805	0.748	0.208	0.188	1	1	3	3	1	1
E. nianguae	0.317	0.868	0.653	0.660	0.652	0.165	0.168	1	1	3	3	2	1

E. nigrum	0.203	0.919	0.800	0.619	0.585	0.182	0.208	1	1	1	1	2	1
E. nuchale	0.370	0.986	0.761	0.753	0.731	0.220	0.221	1	1	3	3	2	1
E. obeyense	0.372	0.969	0.575	0.900	0.781	0.193	0.218	1	2	3	3	1	1
E. okaloosae	0.410	0.883	0.745	0.765	0.721	0.208	0.213	1	1	2	2	1	1
E. olivaceum	0.375	0.825	0.695	0.860	0.768	0.182	0.209	1	1	2	2	2	1
E. olmstedi	0.187	0.864	0.687	0.824	0.705	0.180	0.207	1	1	3	3	2	1
E. osburni	0.239	0.726	0.724	0.795	0.709	0.215	0.186	1	1	3	3	2	1
E. pallididorsum	0.432	1.069	0.739	0.739	0.698	0.212	0.235	1	1	3	3	1	1
E. parvipinne	0.467	1.107	0.691	0.645	0.598	0.192	0.230	1	1	2	2	2	--
E. perlongum	0.205	0.851	0.554	0.766	0.695	0.191	0.191	1	1	2	2	2	1
E. podostemone	0.214	0.922	0.651	0.895	0.738	0.218	0.238	1	1	3	3	1	1
E. pottsi	0.507	1.055	0.925	0.740	0.685	0.198	0.205	1	1	3	3	2	1
E. proeliare	0.416	0.889	0.760	0.591	0.578	0.251	0.246	1	1	3	3	1	1
E. punctulatum	0.371	1.031	0.735	0.771	0.743	0.225	0.224	1	1	3	3	2	1
E. radiosum	0.376	0.884	0.756	0.824	0.775	0.208	0.198	1	1	3	3	2	1
E. rubrum	0.325	0.934	0.772	0.776	0.768	0.205	0.183	1	1	3	3	2	1
E. rufilineatum	0.335	0.687	0.839	0.802	0.707	0.191	0.166	1	1	3	3	2	1
E. rupestre	0.261	0.722	0.659	0.756	0.717	0.265	0.220	1	1	3	3	1	1
E. sagitta	0.333	0.819	0.617	0.709	0.681	0.194	0.183	1	1	3	3	1	1
E. saludae	0.307	1.168	0.644	0.656	0.647	0.194	0.223	1	1	3	3	1	1
E. sellare	0.176	0.938	0.641	0.680	0.690	0.232	0.209	1	1	3	3	1	1
E. serriferum	0.431	1.087	0.673	0.735	0.727	0.229	0.248	1	1	2	2	2	1
E. simoterum	0.341	0.811	0.878	0.724	0.643	0.213	0.193	1	1	3	3	2	1
E. smithi	0.332	1.101	0.578	0.890	0.798	0.198	0.226	1	2	3	3	2	1
E. spectabile	0.315	0.854	0.765	0.823	0.764	0.221	0.214	1	1	3	3	2	1
E. squamiceps	0.360	1.060	0.650	0.852	0.814	0.190	0.234	1	1	2	2	2	1
E. stigmaeum	0.263	0.741	0.761	0.598	0.574	0.221	0.194	1	1	3	3	2	1
E. striatulum	0.365	1.047	0.625	0.841	0.802	0.221	0.214	1	1	3	3	2	1
E. swaini	0.378	0.927	0.834	0.784	0.720	0.207	0.210	1	1	3	3	2	1
E. swannanoa	0.312	0.663	0.763	0.715	0.682	0.218	0.186	1	1	3	3	2	1
E. tetrazonum	0.265	0.730	0.706	0.851	0.757	0.239	0.206	1	1	2	2	2	1
E. thalassinum	0.269	0.833	0.780	0.706	0.664	0.217	0.200	1	1	3	3	1	1

APPENDIX C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	27	28	29	30	31	32	33	34	35	36	37	38	39
E. tippecanoe	0.436	0.778	0.743	0.823	0.800	0.201	0.203	1	1	3	3	1	1
E. trisella	0.410	0.886	0.709	0.588	0.616	0.231	0.232	1	1	3	3	2	1
E. tuscumbia	0.270	1.349	0.849	0.693	0.659	0.158	0.232	1	1	1	1	2	1
E. variatum	0.245	0.845	0.772	0.831	0.756	0.245	0.204	1	1	2	2	2	1
E. virgatum	0.437	0.850	0.624	0.827	0.771	0.212	0.206	1	2	3	3	1	1
E. vitreum	0.153	0.503	0.629	0.676	0.670	0.175	0.198	2	1	3	3	2	1
E. whipplei	0.324	1.003	0.708	0.835	0.701	0.204	0.197	1	1	3	3	2	1
E. zonale	0.310	0.684	0.799	0.678	0.650	0.207	0.205	1	1	1	1	2	1
E. zoniferum	0.440	0.994	0.836	0.547	0.539	0.194	0.218	1	1	3	3	1	1
E. neopterum	0.331	1.167	0.695	0.860	0.812	0.204	0.231	1	1	2	2	2	1
E. (Catonotus) sp.	0.426	0.853	0.662	0.723	0.723	0.204	0.212	1	1	3	3	1	2
E. (Doration) sp.	0.260	0.577	0.791	0.548	0.491	0.192	0.195	1	1	3	3	2	1
E. (Nanostoma) sp. 1	0.357	0.762	0.739	0.734	0.620	0.240	0.211	1	1	3	3	2	1
E. (N.) sp. 2	0.326	0.819	0.708	0.620	0.591	0.219	0.207	1	1	3	3	2	1
E. (N.) sp. 3	0.347	0.964	0.807	0.708	0.677	0.207	0.208	1	1	1	1	2	1
E. (N.) sp. 4	0.357	0.916	0.804	0.633	0.621	0.224	0.202	1	1	2	2	2	1
E. (N.) sp. 5	0.301	0.738	0.785	0.631	0.655	0.229	0.204	1	1	3	3	2	1
E. (N.) sp. 6	0.324	0.749	0.880	0.711	0.634	0.209	0.195	1	1	3	3	2	1
E. (N.) sp. 7	0.307	0.812	0.830	0.697	0.605	0.234	0.203	1	1	2	2	2	1
E. (N.) sp. 8	0.344	0.708	0.786	0.677	0.639	0.222	0.205	1	1	3	3	2	1
E. (N.) sp. 9	0.312	0.701	0.765	0.671	0.633	0.204	0.209	1	1	3	3	2	1

APPENDIX C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	40	41	42	43	44	45	46	47	48	49	50	51	52
P. aurantiaca	1	1	1	2	1	1	1	6	2	1	1	1	1
P. aurolineata	2	1	1	2	2	1	1	5	1	1	1	1	1
P. burtoni	3	2	2	2	1	1	1	6	2	1	1	1	1
P. caprodes	3	2	2	2	1	1	1	6	2	1	1	1	1
P. carbonaria	4	2	2	2	1	1	1	5	2	1	1	1	1
P. copelandi	3	1	1	1	1	1	1	2	2	1	1	1	1
P. crassa	4	1	1	2	1	1	1	3	1	1	1	1	1
P. cymatotaenia	1	1	1	2	1	1	1	3	1	1	1	1	1
P. evides	3	1	1	2	1	1	1	3	2	1	1	1	1
P. lenticula	1	1	1	2	2	1	1	7	1	1	1	1	1
P. macrocephala	2	1	1	2	1	1	1	5	1	1	1	1	1
P. macrolepida	3	2	2	2	1	1	1	4	2	1	1	1	1
P. maculata	3	1	1	2	1	1	1	4	1	1	1	1	1
P. nasuta	2	1	1	2	2	1	1	3	1	1	1	1	1
P. nigrofasciata	2	1	1	2	2	1	1	4	1	1	1	1	1
P. notogramma	4	1	1	2	1	1	1	3	1	1	1	1	1
P. oxyrhyncha	1	1	1	2	2	1	1	3	1	1	1	1	1
P. ouachitae	3	1	1	1	1	1	1	2	2	1	1	1	1
P. palmaris	2	1	1	2	1	1	1	3	2	1	1	1	1
P. pantherina	3	1	1	2	1	1	1	3	1	1	1	1	1
P. peltata	4	1	1	2	1	1	1	3	1	1	1	1	1
P. phoxocephala	2	1	1	2	2	1	1	3	1	1	1	1	1
P. rex	3	2	2	2	1	1	1	6	2	1	1	1	1
P. roanoka	4	1	1	2	1	1	1	2	1	1	1	1	1
P. sciera	2	1	1	2	2	1	1	4	1	1	1	1	1
P. shumardi	3	1	1	1	1	1	1	3	2	1	1	1	1
P. squamata	1	1	1	2	2	1	1	4	1	1	1	1	1
P. tanasi	3	1	1	1	1	1	1	2	2	1	1	1	1

Appendix C.—Character States Used In Numerical Analysis. (Continued)

Species	Characters												
	40	41	42	43	44	45	46	47	48	49	50	51	52
P. uranidea	3	1	1	1	1	1	1	2	2	1	1	1	1
P. (Alvordius) sp.	2	1	1	2	1	1	1	3	1	1	1	1	1
P. (Cottogaster) sp.	4	1	1	2	1	1	1	2	2	1	1	1	1
P. (Imostoma) sp.	3	1	1	1	1	1	1	2	2	1	1	1	1
P. (Odontopholis) sp.	1	1	1	2	1	1	1	3	1	2	1	1	1
P. (Percina) sp.	4	2	2	2	1	1	1	5	2	1	1	1	1
A. asprella	4	1	1	2	1	1	1	5	2	1	1	1	1
A. beani	4	1	1	1	1	1	1	2	2	1	4	1	1
A. bifascia	4	1	1	1	1	1	1	2	2	1	4	1	1
A. clara	4	1	1	1	2	1	1	2	2	1	4	1	1
A. meridiana	4	1	1	1	1	1	1	2	2	1	4	1	1
A. pellucida	4	1	1	1	2	1	1	2	2	1	4	1	1
A. vivax	4	1	1	1	1	1	1	2	2	1	4	1	1
E. acuticeps	2	1	1	2	2	1	1	2	1	1	1	1	1
E. asprigene	1	1	1	2	1	1	1	2	1	1	1	1	1
E. atripinne	1	1	1	1	3	1	1	3	1	1	4	1	1
E. australe	3	1	1	2	2	1	1	1	1	2	1	1	1
E. barbouri	2	1	1	2	1	1	1	2	1	4	1	1	1
E. bellum	1	1	1	2	1	1	1	2	1	1	1	1	1
E. blennioides	1	1	1	2	3	1	1	4	2	1	3	2	1
E. blennius	1	1	1	2	3	1	1	2	2	1	3	1	1
E. boschungi	1	1	1	2	1	1	1	2	2	2	1	1	1
E. caeruleum	1	1	1	2	2	1	1	2	2	1	1	1	1
E. camurum	1	1	1	2	1	1	1	3	1	1	1	1	1
E. chlorobranchium	2	1	1	1	2	1	1	3	1	1	1	1	1
E. chlorosomum	2	1	1	1	2	1	1	2	2	4	1	1	1
E. cinereum	1	1	1	2	1	1	1	3	1	1	3	1	1
E. collettei	1	1	1	2	1	1	1	2	1	1	1	1	1

E. collis	3	1	1	2	1	2	1	1	2	4	1	1	1
E. coosae	1	1	1	1	3	1	1	2	1	1	3	1	1
E. cragini	2	1	1	2	2	1	1	1	2	2	1	1	1
E. davisoni	2	1	1	1	1	1	1	1	1	1	1	1	1
E. ditrema	1	1	1	2	1	1	1	1	1	2	1	1	1
E. duryi	1	1	1	1	3	1	1	2	1	1	4	1	1
E. edwini	1	1	1	2	1	2	1	1	1	1	1	1	1
E. etnieri	1	1	1	1	3	1	1	3	1	1	4	1	1
E. euzonum	1	1	1	2	2	1	1	2	3	1	1	1	1
E. exile	1	1	1	2	2	2	1	2	1	2	1	1	1
E. flabellare	1	1	1	2	3	1	1	3	1	3	1	1	1
E. fonticola	4	1	1	2	2	2	2	1	2	4	1	1	1
E. fricksium	1	1	1	2	2	1	1	2	2	1	1	1	1
E. fusiforme	1	1	1	2	2	2	1	1	2	3	1	1	1
E. gracile	2	1	1	2	2	2	1	1	2	1	1	1	1
E. grahami	1	1	1	2	2	1	1	1	1	4	1	1	1
E. histrio	3	1	1	2	3	1	1	2	1	1	3	1	1
E. hopkinsi	2	1	1	2	2	1	1	2	2	1	1	1	1
E. inscriptum	2	1	1	2	3	1	1	2	2	1	1	1	1
E. jessiae	1	1	1	2	1	1	1	2	2	1	3	1	1
E. jordani	1	1	1	2	1	1	1	2	1	1	1	1	1
E. juliae	1	1	1	2	3	1	1	2	1	1	1	1	1
E. kanawhae	1	1	1	2	3	1	1	2	3	1	1	1	1
E. kennicotti	2	1	1	2	2	1	1	2	1	4	1	1	1
E. lepidum	1	1	1	2	1	1	1	2	1	4	1	1	1
E. longimanum	2	1	1	1	3	1	1	2	1	1	1	1	1
E. luteovinctum	1	1	1	2	2	1	1	2	2	3	1	1	1
E. maculatum	1	1	1	2	1	1	1	3	1	1	1	1	1
E. mariae	1	1	1	2	3	1	1	2	1	1	1	1	1
E. microlepidum	1	1	1	2	1	1	1	2	1	1	1	1	1
E. microperca	2	1	1	2	2	2	2	1	2	4	1	1	1
E. moorei	2	1	1	2	1	1	1	2	1	1	1	1	1